QUANTITATIVE GENETICS IN FISH BREEDING

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Doctor of Philosophy

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1981

DECLARATION

I, Brian P. Kinghorn, declare that this thesis has been composed by myself and that the experimental work and analyses described herein have been carried out by myself, except where expressly noted.

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ABSTRACT

Part I. The fish farming industry in Europe.

A brief description of the industry in Europe is given with emphasis on present and future levels of production, major areas of research and patterns of development within the industry.

Part II. A review of quantitative genetics in fish breeding.

In recent years there has been increasing research activity in quantitative genetics of farmed fish, especially relating to the salmonid species. This review covers all major aspects of quantitative genetics which are of direct or potential relevance to improving the efficiency of production of farmed fish.

Part III. Genetic variation in food conversion efficiency and growth in Rainbow trout.

This type of work has not previously been undertaken because of difficulty in measuring food consumption of fish on a sufficiently large scale. This problem was overcome by the development of a system to estimate food consumption through consideration of metabolic rate (via oxygen consumption) and the energy component of growth. 231 full sib families of young Rainbow trout were tested in this system over a two year period. The family mean heritabilities of food conversion efficiency, growth and food consumption were estimated at 3 $\pm$ 10%, 26 $\pm$ 12% and 41 $\pm$ 13% respectively. Phenotypic and genetic correlations of family means for these traits were all close to unity. It is concluded that selection for improved food conversion is of little value.

PART I

THE FISH FARMING INDUSTRY IN EUROPE

PART I

THE FISH FARMING INDUSTRY IN EUROPE

1. INTRODUCTION

Fish farming in Europe was probably of some signficance in the middle ages when coarse fish were reared or merely stored in natural or man made ponds. Increased sea fishery and improved distribution probably caused a decline in these activities.

Fish farming as a significant source of food was established by 1950 when carp was produced at a moderate level in Eastern Europe, and Denmark was producing over 2 000 tonnes (t) of Rainbow trout per year. Growth in total European production has been most marked over the last decade and output is currently doubling over a period which is probably less than 10 years. This high rate of change makes it difficult to ascertain the overall state of the industry. Production figures quoted are compiled from one or more sources, including personal communications. Major sources are listed in section 5.

2. PRESENT AND FUTURE LEVELS OF PRODUCTION

2.1. Carp

Production in Europe in 1975 was 360 000 t, of which European U.S.S.R. produced 200 000 t, Eastern European countries (Poland, Yugoslavia, Romania, Hungary, Czechoslovakia, East Germany and Bulgaria) produced 150 000 t and France and West Germany produced 13 000 t. There seems to be potential for greatly increasing production both through intensification (supplementary feeding, fertilisation of earth ponds and polyculture)

and expansion. Carp tolerate poorer quality water (low dissolved oxygen, suspended matter etc.) than, for example, Rainbow trout, such that the scope for number and size of farms is wide. During the foreseeable future, the level of production will probably be more limited by economic factors than by biological factors.

2.2 Rainbow trout.

At the end of the last century, Rainbow trout were introduced into Denmark and production in earth ponds became established in the western and central part of Jutland. Total export figures for 1959 (6044 t), 1969 (10 747 t) and 1980 (17 500 t) suggest a steady growth in production (home consumption is approximately 5% of these figures). However, measures to protect the environment seem likely to limit future production to little over the 1980 level.

In Europe as a whole, production of Rainbow trout reached 95 000 t in 1980, with Italy (20 000 t), France (20 000 t), Denmark (17 500 t), Germany (11 000 t) and Spain (10 000 t) as the major producers. Production systems include rearing in concrete raceways (Italy, France), earth ponds (Denmark, West Germany), concrete ponds (UK and others) and sea cages (Norway). In general, portion sized fish (200-300 g) are produced. Potential production of Rainbow trout in fresh water is limited by availability of water of suitable quality. In Italy and France, only 15-30% of potential water resource was unexploited in 1975 and this may reflect the situation in Europe as a whole. However, increased production through recycling of water, improved disease control, genetic progress and other technology, probably puts the biological limit at several times the current levels of

production. Obviously economic factors are involved here, and in fact poor market demand is currently having a restrictive effect.

Production of Rainbow trout in sea cages started in Scotland and Norway about ten years ago, and Norwegian production reached 2 700 t in 1979. This system produces 1.5-4 kg fish with pink flesh similar in quality to that of salmon. Production in Norway is presently limited by marketing problems (this is a new product) but there seems great potential for farming Rainbow trout in this way. Denmark has a small but expanding production of steelhead trout farmed in the sea.

2.3. Salmon.

Production of Atlantic salmon reared for up to 2½ years in sea cages has developed principally in Norway and Scotland since the late sixties. Production is currently about 5000 t in Norway and 600 t in Scotland with 1985 projections of 20 000 t and 1500 t respectively. Output is low but expanding in Ireland and France. With the exception of Norway, potential production would appear to be limited by the number of suitable sea sites, but it is not easy to determine what such limits may be, due to advances in cage design and other technology. Established markets for wild caught salmon have proved to be reliable outlets for the quality farmed product, but there are some indications that market saturation may soon be a problem. West Germany, Sweden, Denmark, Italy and France are major importers of farmed salmon.

France produces about 100 t of Coho (Pacific) salmon raised in net cages. The potential for this industry is about 3000 t.

2.4. Marine fish.

Extensive raising of mullet, sea bass, gilthead and eel in fenced lagoons is established on the North Adriatic coast of Italy. Many similar sites are unexploited in France. This industry has been based on capture of wild young. However, sea bass and gilthead fingerlings are now being artificially hatched and grown. Present production includes 4 000 t of mullet (1980) and figures for the other three species are probably similar. There seems to be potential to increase production to over 90 000 t through supplementary feeding and intensification.

Experimental work on the culture of various marine flatfish and roundfish has long been underway in Britain, Norway and France. The major problem encountered has been first-feeding on expiry of the yolk sac of juveniles, and similar problems at later stages. Breeding in captivity has been achieved notably in plaice, turbot, Dover sole and cod. Commercial farming of turbot is at an early stage, and production of Dover sole may soon be viable.

The potential size of this industry is difficult to predict as the required level of technology is presently high. The large governmental research input involved suggests some high expectations.

2.5. Eels.

Intensive production of eels in freshwater is a young but rapidly expanding industry. Tolerance to crowding and poor water quality has resulted in highly intensive culture of eels in warm effluent water from various industries. Present production from such systems is probably low. In Italy, eels are grown in fenced lagoons as outlined above (2000 t

in 1977) and in intensive fresh water farms (1200 t in 1980). As eel farming started in Italy in 1969, rate of growth should be high.

All eel farming operations are presently based on capture of wild elvers as attempts at breeding in captivity have failed. West Germany is a major importer of both wild caught and farmed eels.

2.6. Others.

Farming of catfish (Brown bullhead) was established in Italy in 1971 and current annual production is 1400 t. Tench, roach, pike, brown trout and some others are cultured in small quantities. Some species (notably sturgeon species) are raised for release as fingerlings.

3. RESEARCH AND DEVELOPMENT

With few exceptions, research work seems to proceed with little international coordination. Even within nations coordination can be poor, with work being carried out independently by agricultural institutions, fisheries institutions and private industry. As with most animal industries, there is room for improvement in communication and cooperation between research bodies.

Important areas of research and development include the following:

3.1. New species and systems.

Investigation of novel production systems for rearing both established and novel farmed species is the most fundamental area of research. Vast resources for direct or indirect use in fish farming may lie in domestic, agricultural, fisheries

and industrial waste. Some species might prove to be well suited to farming if biological and/or marketing problems can be overcome. For example, the halibut shows promise of being an extremely productive fish under cultivation, but problems have been encountered in first-feeding of young, and holding facilities for slaughter stock may require independent development due to the large size of adult fish.

3.2. Genetics.

Development of genetic techniques and estimation of genetic parameters in farmed populations can both contribute greatly to the efficiency of genetic improvement programs. Large organisations investing in fish farming have generally made available the results of valuable research. However, when large investments are made in genetic improvement programs, such cooperation might not exist. The poultry industry provides an analogy here. This outlines the importance of establishing government operated genetic improvement programs for the benefit of all producers, but with close attention to the biological and economic relevance to each farming area. Techniques for deep freezing semen (achieved in Rainbow trout and Atlantic salmon) and fertilized eggs could greatly facilitate hygienic transfer of genetic material and can be usefully employed in selection work.

3.3. Nutrition.

The potential for farmed fish is largely based on the high efficiency of food conversion which can be achieved (0.53 calories edible product per calorie metabolisable energy of food for Rainbow trout, versus 0.25 for pigs, 0.18 for poultry and 0.3 for milk production).

Development of cheap sources of food, with particular reference to digestible protein from soya beans, algae,

yeasts etc. is a high priority for carnivorous farmed fish. The technologies of processing, storing and feeding are all involved in improving efficiencies in all branches of intensive fish farming. In most species there can be room for improvement of gross food conversion efficiency through improved feeding techniques.

Many other sources of foodstuff are unexploited, especially byproducts of fisheries and animal slaughter, and a development of such exploitation is required.

3.4. Equipment and Techniques.

Much of the development here has come from within the commercial sector (with some notable exceptions in marine species) and this is likely to continue to be the case. Current areas of investigation include aeration and recycling of water (which can increase biological limits to production considerably), sea cage design (with emphasis on durability, anti-biofouling and ease of handling) feeding systems, and automated systems for handling fish.

3.5. Disease control.

Disease is a major problem, especially under intensive rearing, and effective control could by itself improve total production considerably. Present investigation includes use of vaccines, defining the role of stress and genetic improvement of disease resistance. However, the most important factor here is probably the implementation of effective policies controlling the transmission of disease.

3.6. Control of development.

In most farmed species the onset of sexual maturity is accompanied by a marked reduction in growth and a deterioration of meat quality. Induction of sterility can overcome these problems and permit growth to a higher slaughter weight, giving access to more favourable market prices. Promising techniques in this area involve use of hormones, induction of triploidy, immunosuppression of gonads and physical castration.

Other areas of interest here are the induction of smoltification in Atlantic salmon and control of spawning in all species. Artificial spawning in most warm water species requires hormonal intervention. The induction of out of season spawning in salmonids is an aim of a number of research groups.

3.7. Ocean ranching.

Release of Pacific salmon fingerlings which return to point of release as adults is now established principally in North America, Japan and U.S.S.R.. Ocean ranching of Atlantic salmon is established within conservation programs and is only practised for profit in Iceland where a total ban on the wild sea fishery is in effect in territorial waters. Much has still to be learned from basic research on technique and stocks utilized. Commercial viability of ocean ranching may be dependent on control of the illegal wild fishery and further restrictions on the legal fishery.

4. CONCLUSIONS

There is little doubt that fish farming in Europe will grow considerably over the next few decades. The pattern of this growth will be highly sensitive to intervention by

governments, and as such, an opportunity exists for guiding this industry into the most efficient and socially valuable position. It seems that this opportunity is not being fully exploited in many European countries.

The Norwegian government has put a restriction on the maximum size of sea farms such that small, sometimes family based farms are encouraged. Production efficiency is enhanced through ownership motivation at the possible expense of a certain lack of regulation and discipline. Social benefits in sometimes very remote areas are evident here. This pattern of development requires government back up in training and extension services, market assurance, regulated feed supply and adequate insurance cover.

However, relationships between large fish farming companies and the smaller producers are often very good, with co-operation in contract fattening and technical support. This path of development may be more efficient in production terms with additional advantages in research and development output by large companies. Yet where such cooperation and government support are both poor, new investors can be obliged to integrate vertically, processing their own feed and developing market outlets. This in turn can put a lower limit to the size of a viable unit. Thus, whatever the pattern of development in the industry, it is often advisable for governments to provide back up services as outlined above, possibly sponsored from within the industry, in order to provide a stable environment for small producers. An alternative or supplement to this can be the formation of cooperatives by producers themselves. This is most realistic in branches of the industry which are reasonably well established.

It is becoming evident that the need to develop markets to absorb increased production has been badly neglected in several species, especially the salmonids. Per capita consumption of farmed fish is generally very low and there is much room for expansion of the market. Low prices due to restricted demand do not seem to have increased consumer awareness of farmed species. Positive promotional policies are required on a large scale to ensure reliable outlets for the higher production which is forecast.

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PART II

A REVIEW OF QUANTITATIVE GENETICS IN FISH BREEDING

PART II

A REVIEW OF QUANTITATIVE GENETICS IN FISH BREEDING

1. INTRODUCTION

Animal breeding theory has only recently been applied to fish culture, and is not yet widely practised. Research in quantitative genetics of fish is mostly restricted to salmonids (North America, Norway and France) and carp species (Israel and U.S.S.R.).

Commercial interest in breeding programs is overshadowed by continuing efforts to develop optimum husbandry techniques, and few companies practise anything other than mass selection.

2. CHOICE OF SPECIES AND STRAIN FOR CULTURE

The choice of species or strain to use in a given culture system is one of the most fundamental genetic problems. Unlike farm mammals and poultry, retail prices of fish meat can vary greatly between animals of similar type. For example, Dover sole can command a price over five times greater than that of plaice (Kerr and Kingswell, 1977). In view of this, any marginal differences in the quantitative efficiency of meat production become insignificant.

In a trial involving five species of salmonid (Atlantic salmon, Pink salmon, Arctic char, Sea trout and Rainbow trout) farmed in sea cages, Gjedrem and Gunnes (1978) conclude that the Pink salmon is most efficient to rear for the 0.5-1.5 kg "pan size" market, Rainbow trout for the 3-4 kg market and Atlantic salmon for the 4-5 kg market.

In Britain, the turbot has been selected by the White Fish Authority and several industrial companies as the main contender for the first farmed wholly-marine finfish (Jones, 1972). This was after earlier work had been carried out on other flat-fish, notably plaice. The advantages that turbot has over plaice are higher market value, greater tolerance to crowding, faster growth and cheaper feeding costs (Reay, 1979).

Wohlfarth et al. (1975) compare the attributes of the European and Chinese races of carp and indicate that the European race is more suitable for semi-intensive cultivation in cleaner waters, whereas the Chinese race is superior where the organic content of the water is high.

In two trials, different species of salmonid were reported to be acid tolerant in the following rankings: Brook trout, Brown trout, Atlantic salmon, Rainbow trout (Muniz and Grande, 1974); Brown trout, Arctic char, Rainbow trout (Edwards and Hjeldnes, 1977). This information bears significance in the choice of species for culture in waters of low pH.

Differences in performance between strains within species have also been documented. Chevassus (1976) has estimated the coefficient of variation in mean fingerling weight between strains of Rainbow trout to be 20%. Refstie and Steine (1978) report genetic variation in length and weight after the freshwater phase in 32 Norwegian strains of Atlantic salmon. Gunnes and Gjedrem (1978) report genetic variation in growth during two years in the sea in 37 Norwegian strains of Atlantic salmon. In this case the largest strain was more than twice the weight of the smallest strain. Fish farm (5 in number) by strain interaction was significant but sufficiently small to

justify the adoption of a singular national policy on strain selection.

However, Klupp et al. (1973) have reported a figure of 0.67 for the genetic correlation between growth in floating nets and growth in ponds for 3 strains of Rainbow trout and their crosses. This indicates a danger in general interpretation of strain comparison data.

Strain differences have also been reported with respect to disease resistance (Gjedrem and Aulstad, 1974, in Atlantic salmon, and Hines et al, 1974, in common carp), egg size, egg number, egg volume and eggs per 100 grams body weight (Gall, 1975, in Rainbow trout).

Calaprice (1976) suggests that the shad and the alewife might be more biologically efficient than the various species of Pacific salmon with respect to "sea ranching", where fingerlings are released into rivers and harvested as adults on their return to the same rivers after a period at sea. Once again, market demands are such that this is unlikely to be commercially viable in the foreseeable future.

3. SELECTION WITHIN POPULATIONS

In fish, offspring of individual males or females rarely number less than a thousand from any one spawn. With fertilisation taking place in vitro, the number of full sib families can be made to equal the product of the number of breeding males and the number of breeding females. This type of breeding structure can be useful in the estimates of dominance genetic variance, and the accuracy of selection can be increased due to the extra information available from half sibs of common dam. This latter feature has not yet been exploited in a selection program.

The very high fecundities involved have contributed to an optimism about the value of selection in fish (Gjedrem, 1975 a and 1976b; Purdom, 1972a) and shellfish (Longwell, 1976). However, some points must be considered in this light:

i) Under natural conditions, a very small proportion of fish larvae survive to contribute to the next generation. This implies that the need for genetic "buffering" for high fitness is less than, for example, domestic mammals. If this were so, a drop in fertility and viability on selection for characters not associated with fitness is expected. However the literature indicates that pre-adult mortality in nature is largely dictated by random environmental factors (see, for example, Cushing, 1977).

ii) Aitken (1934) has shown that genetic variance within a population is reduced with selection of increasing intensity. The limit to selection response is maximised by selecting 50% of individuals for breeding (Robertson, 1960). This illustrates a danger in prolonged selection for one trait at a very high intensity. The use of multitrait selection, either by independent culling levels or by an index will minimise long term restrictions on selection response.

iii) The use of a small number of individuals for breeding purposes (as is normally practised due to high fecundity) gives rise to the possibility of inbreeding. Allendorf and Utter (1979) conclude that inbreeding is the cause of reductions in variation at a number of polymorphic loci in a stock of Rainbow trout. Kincaid (1972) has estimated a reduction in fitness traits (5-15%) and in growth (5-10%) for each 10% increase in the inbreeding

coefficient of Rainbow trout. Gall (1969) has noted that the death rate of Rainbow trout fry and fingerlings increases upon inbreeding. Kincaid (1976) has demonstrated that through effects on several traits inbreeding depression in Rainbow trout caused a reduction in weight of fish produced per year of 36.6% (F = 0.25) and 65.4% (R = 0.375), (see table 3.1). At the commercial level, this is a problem which requires the recording of parentage and cooperation among producers to permit the migration of genetic material under hygienic conditions.

Table 3.1. Effects of inbreeding in Rainbow trout (Kincaid, 1976). All figures are given in percentage units.

Coefficient of inbreeding	25.0	37.5
Increase in number of crippled fry	37.6	191.5
Reduction in food conversion efficiency	5.6	14.9
Reduction in survival to 147 days	14.6	29.7
Reduction in growth to 147 days	6.0	13.4
Reduction in growth to 304 days	23.2	33.5
Reduction in number of fish produced per year	17.4	47.9
Reduction in weight of fish produced per year	36.6	65.4

A major problem in the operation of a selection program is that young fish cannot be marked until they reach a certain size. This means that full sib families must be kept separate from each other until this stage (at least six months in salmonids) if family data are to be used. A restricted solution to this problem is given by Hedgecock (1976), who suggests the use of biochemical

polymorphisms to "mark" families such that some mixing of stock can be carried out after fertilisation is complete.

3.1. Realised response to selection.

An early account of artificial selection in Rainbow trout is given by Lewis (1944) who reports responses in early spawning, egg number and yearly weight. Intensive selection in Rainbow trout over 23 years (6-7 generations) is reported to have had large effects on growth rate, egg production and early spawning (Donaldson and Olson, 1955), but this is confounded with changes in management and facilities.

Gjerde (personal communication) has found realised response to selection for slaughter weight (3½ years old) in two year classes of Atlantic salmon (Table 3.2). The estimate relating to the 1981 slaughtering season is biassed downwards due to unintentional selection in the control population. A realised response of about 3 percent per year under the breeding program involved corresponds to a realised heritability of about 15-20%.

Table 3.2. Realised response to one generation of selection for slaughter weight in Atlantic salmon (Gjerde, personal communication). The 1979 control population was derived from wild caught parents, the 1981 control population was derived from hatchery reared unselected parents.

Slaught. season	Mean weight (kg)		Realised response (%)	
	Progeny of selected parents	Progeny of control parents	Per gen.	Per year
1979	4.27±0.01	3.73±0.02	14.5	3.6
1981	5.08±0.01	4.59±0.17	10.7	2.7

Moav and Wolfarth (1978) report no response to selection for high growth rate in carp over five generations, but a relatively strong response to selection for slow growth over three generations. They suggest that selection for high growth has reached a plateau involving overdominance, which maintains genetic variation. Subsequent selection between families resulted in considerable progress while maintaining a large genetic variance.

Longwell (1976) has reported a realised heritability of 93% for weight at 33 days post setting of the oyster Crassostrea virginiea based on one generation of selection. No control population is described.

Von Limback (1970) and Bridges (1973) have reported responses of approximately 40% per generation to selection for and against 150 day weight in Rainbow trout, but do not quote any genetic parameters. Kincaid (1977) reports a 30.1% per generation improvement in 147 days post fertilisation weight of Rainbow trout over three generations of selection on family means. This represents a realised heritability of family means of 26%, corresponding to a realised heritability of 6% for individuals. This response is in fair agreement with estimations by Kincaid (1972) for heritability of family means in the same stock of fish (29%±11% and 26%±12% on the basis of parent-offspring regression and half-sib correlation, respectively).

3.2. Estimation of genetic parameters.

Estimates of genetic parameters for economically important traits are becoming available in the popular species. These will be dealt with according to trait.

3.2.1. Growth

Table 3.3 presents some estimates of heritabilities and coefficients of variation of growth traits. In salmonids, there is a general tendency for heritability of weight to increase with age. This could be due to a diminishing maternal influence, as found for survival traits in splake hybrids (Salvelinus fontinalis x S. namaycush), by Ayles (1974).

Estimates of the heritability of weights after the fingerling stage appear to average approximately 20%, with a coefficient of variation of approximately 30%. Gjedrem (1975a) has used estimates of heritability (20%), coefficient of variation (40%), selection intensity (2.66 standard deviations), and generation interval (3 years) to predict a 7% per year improvement in growth through a hypothetical selection program in Rainbow trout. This compares favourably with expected responses to selection in other domestic animals.

The rate of growth of Atlantic salmon fingerlings is of special importance as this is strongly associated with the proportion of fish which smoltify at one year of age. Salmonids first become tolerant to sea water as smolts.

In nature, smoltification takes place seasonally at 2, 3 or more years of age, whereas cultured salmon smoltify at one year (S1's) or at two years (S2's). The ability to smoltify at one year of age is a very desirable trait, as, at smoltfication, S2's are little better grown than their S1 contemporaries were at the same stage of development.

Table 3.3. Estimated heritabilities (h^2), their standard errors (S.E. (h^2)) and coefficients of variation (C.V.) for various growth traits in fish and shellfish. All heritabilities are estimated from the sire component of variance of a sib analysis except for those estimated marked (d), where the dam component of variance was used.

Species	Measure	h^2 (%)	S.E.(h^2) (%)*	C.V. (%)	Author
Rainbow trout	150 day weight	9	10	30	Aulstad et al. (1972)
Rainbow trout	150 day weight	6	-	-	Kincaid (1977)
Rainbow trout	140 day weight	6	(NS:P>5%)	52	Refstie (1980)
Rainbow trout	fingerling weight	5-38(d)	10	40	Chevassus (1976)
Rainbow trout	280 day weight	29	20	33	Aulstad et al. (1972)
Rainbow trout	2½ year weight	17	(P<5%)	36	Gunnes & Gjedrem (1981)
Rainbow trout	2½ year weight	21	10	30	Gjerde (1981a)
Rainbow trout	2½ year post spawning weight	21(d)	5	23	Gall (1975)
Atlantic salmon	190 days post first feeding wt.	8	(P<5%)	78	Refstie et al. (1978)
Atlantic salmon	3½ year pre-spawning weight	31	(P<1%)	30	Gunnes & Gjedrem (1978)
Atlantic salmon	3½ year pre-spawning weight	37	11	28	Gjerde (1981a)
Rainbow trout	150 day length	16	14	12	Aulstad et al. (1972)
Rainbow trout	140 day length	20	(NS:P>5%)	17	Refstie (1980)

Table 3.3. Continued.

Species	Measure	h^2 (%)	S.E.(h^2) (%)*	C.V. (%)	Author
Rainbow trout	280 day length	37	23	12	Aulstad et al. (1972)
Rainbow trout	2½ year length	23	(P<5%)	12	Gunnes & Gjedrem (1981)
Rainbow trout	2½ year length	16	10	7	Gjerde (1981a)
Atlantic salmon	190 days post 1st. feeding length	12	(P<5%)	26	Refstie et al. (1978)
Atlantic salmon	3½ year pre-spawning length	28	(P<5%)	10	Gunnes & Gjedrem (1978)
Atlantic salmon	3½ year pre-spawning length	26	10	9	Gjerde (1981a)
Plaice x flounder hybrid	Growth at ~6 months	~0	-	-	Purdom (1976)
Carp	Growth to 8 months	~0	-	-	Moav (1965)
Carp	Growth to 8 months	0	-	-	Moav & Wohlfarth (1976)
C. virginica	2 week larval weight	24	-	-	Longwell (1976)

* some authors quote the significance of the sire mean square instead of the standard error of the heritability estimate.

Bimodal distributions of weight in Atlantic salmon fingerlings have been observed (Thorpe, 1977). Refstie et al. (1977b) have estimated the heritability of smoltifcation at one year to be 0.06, with a high sire x dam interaction (implying a high dominance genetic variance) and with additive genetic variance greater between strains than within strains. Egg diameter is not correlated with smoltification at one year (Thorpe, 1977), but paradoxically, stocking density is positively correlated with this trait (r = 0.03-0.27) (Refstie et al., 1977b). Ritter (1975) has reported that S1's mature later than S2's. If this reflects the nature of the underlying genetic correlation then this would be a favourable phenomenon.

It has been postulated that the low heritability of growth in carp represents a selection plateau caused by a long history of mass selection (Moav and Wohlfarth, 1973). However, this cannot be the reason for the apparently low heritability in plaice x flounder hybrids (Purdom, 1976) which have only recently been domesticated. The repeatability of monthly increments in length of individually housed plaice x flounder hybrids was 8%, indicating a low heritability for growth in length despite the absence of competition effects. No reference has been found to heritability estimates from population data in flatfish.

Reviewing several papers, Newkirk (1980) concludes that the heritability of larval growth rate in the oyster Crassogrea virginica is in the range 0.25 to 0.5.

In both Atlantic salmon and Rainbow trout the genetic correlation between weight and length at various ages

is consistently close to unity (Refstie and Steine, 1978; Gunnes and Gjedrem, 1978; Refstie, 1980 and Gunnes and Gjedrem, 1981). As length is generally more heritable than weight (see table 3.3), the correlated response in weight due to selection on length is expected to be greater than the direct response to selection on weight.

A major problem for the Atlantic salmon industry in Scotland and Ireland is the high proportion (about 30%) of grilse individuals which mature after only one year in the sea. Naevdal et al. (1978) have observed differences between strains in stage of maturity, and Gjerde (1981 a) reports that maturity score at slaughter is highly variable (C.V. = 35%) and highly heritable (h^2 = 42±9%) indicating that selection to reduce the proportion of grilse should meet with success.

When using "borrowed" estimates of growth trait heritabilities in the formulation of a selection index or for prediction of response to selection, it must be borne in mind that growth in fish can be more sensitive to environmental effects than growth in warm - blooded animals. Growth at intermediate stages in most species of fish can be virtually halted for a long period of time by restricted feeding, whereas young mammals can only withstand a relatively short period of no growth. This property of fish growth indicates an increased scope for environmental variation and illustrates an increased danger in reliance upon "borrowed" genetic parameters.

3.2.2. Carcass traits.

Gjerde (1981a) reports heritabilities close to zero for dressing percent and flesh colour in both Atlantic salmon and Rainbow trout. Belly thickness (thick is favourable) is moderately heritable in both species

(17±6% each), however, this trait was found to have a high genetic correlation with body weight (92±7%). In both species, the genetic correlation between gutted weight and whole body weight was close to unity, with similar heritabilities for each trait within each species.

Ayles et al. (1979) report additive and non-additive genetic variation in lipid content between strains of Rainbow trout. Results from part III of this thesis indicate that percent fat may be moderately heritable in young Rainbow trout.

3.2.3. Food conversion efficiency.

This is of particular importance in those fish species which are obligate carnivores in nature, e.g. salmonids, flatfish, eels, and yellowtail. Common carp, Tilapia spp. and most other cyprinids are predominantly herbivores or detritus feeders in nature, and any artificial feeding usually involves manure or fertilizer which are considerably cheaper than, for example, pelleted feeds for salmonids.

Being poikilothermic (cold-blooded), fish use a minimum of energy on maintenance and as such are likely to have less absolute genetic variation in basal metabolic rate than domestic mammals or poultry. However, there is scope for variation in food conversion efficiency (F.C.E.) due to differences in activity, efficiency of digestion, growth rates of the different tissue types and other factors.

Until recently there has been no population information on F.C.E. suitable for genetic analysis. This is due to difficulties involved in direct estimation of food consumption on a large scale. Kinghorn (1980) reports the

development of a system to estimate food consumption in 33 tanks at a time through a consideration of energy metabolised (via oxygen consumed) and the energy component of growth. Part III of this thesis concludes that F.C.E. in young Rainbow trout is lowly heritable (heritability of family means =3±10%, coefficient of variation = 8.3%).

Edwards et al. (1977) and Refstie and Austreng (1981) showed no significant family x diet interaction in trials involving Rainbow trout on feeds of various carbohydrate levels. This indicates that selection for the specific ability to utilise a cheaper, high carbohydrate food would meet with little success.

3.2.4. Reproductive performance.

In the past, a lot of effort has been put into selection for early maturity (Lewis, 1944; Donaldson and Olson, 1955). In view of present trends this is thought to have been the wrong policy (Purdom, 1976) as adult growth is severely restricted at maturity both through routing of nutrients to the gonads and a depression of appetite. Meat quality is also reduced at this stage (Mills, 1970).

Gall (1975) has presented estimates of some genetic parameters relating to reproduction in Rainbow trout. Table 3.4 shows the heritabilities of, and correlations between body weight of dam, egg size, egg number, egg volume and eggs per 100 g dam body weight. All estimates are derived from full sib family components of variance and covariance. Coefficients of variation for the five traits range from 18% to 28%.

Of note here is that genetic correlations between body weight, egg size, egg number and egg volume are all significantly positive with the exception of egg size and egg

Table 3.4. Genetic parameters relating to reproduction in Rainbow trout (Gall, 1975). All estimates are derived from the full sib family components of variance and covariance.

	B.W.	E.S.	E.N.	E.V.	E./W.
B.W.	0.21±0.05	+0.46±0.13	+0.39±0.14	+0.56±0.11	-0.61±0.10
E.S.	+0.19	0.20±0.05	-0.09±0.17	+0.55±0.12	-0.47±0.13
E.N.	+0.35	-0.15	0.19±0.05	+0.77±0.07	+0.41±0.10
E.V.	+0.43	+0.45	+0.78	0.20±0.05	-
E./W.	-0.50	-0.26	+0.51	-	0.20±0.05

B.W. - body weight of dam; E.S. - egg size; E.N. - egg number; E.V. - egg volume; E./W. - eggs per 100 g body weight. Figures on the main diagonal are heritabilities, figures above the main diagonal are genetic correlations and figures below the main diagonal are phenotypic correlations.

number whose genetic correlation is not significantly different from zero. All these traits have heritabilities close to 0.2, and are of positive economic value. Chevassus (1976) has reported a phenotypic correlation of 0.65 (significantly positive, $P<1\%$), between volume of eggs and the average length of the fry 30 days after hatching.

Although individual selection of females on spawning traits is not practical, information from relatives can be incorporated in an index. In the light of the results quoted, selection for increased body weight is unlikely to decrease reproductive fitness.

3.2.5. Resistance to disease.

With the increase of salmonid culture over the last decade, there has been an increase in variety and incidence of diseases. Strict health control is practised by commercial producers and legislation on conduct is becoming operative.

Strain differences in resistance to fish pox and swim bladder infection exist in carp (Hines et al. 1974). It was concluded that susceptibility to both these diseases is controlled by recessive genetic factors.

Amend and Nelson (1978) have reported significant variation between full sib families of Sockeye salmon in resistance to infectious haemopoetic necrosis virus. Gjedrem and Aulstad (1974) estimate the heritability of resistance to vibrio disease in Atlantic salmon at 12%±6%. The coefficient of variation of family means for this trait was close to unity, Although this is biassed upwards due to crossinfection between fishes, it was concluded that very high selection differentials could be realised. Ayles (1974) reports a heritability of 76%±28% for resistance to blue sac disease in hybrid splake alevins (Salvelinus fontinalis x S. namaycush).

Longwell (1976) quotes two cases of a response to natural selection for disease resistance in the oyster C. virginica.

Although the ideal solution to the disease problem might be to develop resistant strains through selection, this is not something which commercial producers will entertain lightly. Unless government organisations carry out this work, other methods must be considered, such as cross-breeding, with testing of cross progeny away from the sites of commercial production.

3.2.6. Survival and tolerance.

The proportion of phenotypic variance in mortality that is due to maternal effects (Vm/Vp) in splake hybrids is high in uneyed eggs (78%±22%), and reduces through eyed eggs (68%±24%) to alevins (40%±19%) (Ayles, 1974). The residual variation is largely due to additive genetic differences (the heritability of alevin mortality was 41%±18%), which in this case appears to be related to resistance to blue sac disease. Kanis et al. (1976) have estimated the heritability of mortality of eyed eggs at 5-11% (Atlantic salmon), 15-20% (Rainbow trout) and mortality of fry at 1-4% (Atlantic salmon), 6-14% (Rainbow trout). Kincaid et al. (1977) report a null response in hatchability and fry survival after three generations of selection in Rainbow trout.

The economic value of improving these traits of early mortality may not justify the selection effort. The proportionate cost of maintaining brood stock is low compared with domestic mammals and the resulting gain in selection intensity is also low.

However, mortality at later stages can be more important economically and probably deserves more attention. As causes can usually be identified as a disease, or some environmental factor, it is more efficient to look at these specifically and not generalise on mortality per se.

In salmonids, genetic variation in tolerance to acid water has been described between strains (Edwards and Hjeldnes, 1977; Swartz et al. 1978; Muniz and Grande, 1974) and within strains (Robinson et al. 1976; Gjedrem, 1976 a). Gjedrem (1976 a) gives estimates of the heritability of tolerance to acid water in Brown trout ranging from 0.09-0.27. Edwards (1978) describes a Norwegian

project involving selection of a strain of Brown trout for high tolerance to low pH. Successful development in this field will widen the scope of trout "ranching" to the many Norwegian lakes which have become acidic due to atmospheric pollution (Edwards, 1978), and to American rivers which are polluted by sulphuric acid from coal mines (Robinson et al. 1976).

Salmonid culture is often restricted by the presence of various pollutants, low oxygen concentration, temperature fluctuations and other environmental effects. Although development of tolerant strains would greatly widen the scope of production, little work is done in this field while suitable farm sites remain unexploited.

3.2.7. Recapture frequency.

In a experiment involving release and recapture of tagged Atlantic salmon, significant differences were found between full sib families for recapture frequency (Carlin, 1969). This indicates a possible genetic variation in the ability to return to the river of origin.

3.3. The effects of competition on selection for growth traits.

The effect of competition between fishes on growth can be considerable, especially under farming conditions. From a very early stage, salmonids develop territorial behavior and hierarchies (Mills, 1970) which are most predominant when food is scarce (Symons, 1967). Distri-

butions of weight and length in carp fingerlings can be very highly positively skewed (Moav and Wohlfarth, 1973). The coefficient of variation of growth in plaice was reduced severalfold by individual housing (Purdom, 1972 a)

A problem here is that in a competitive environment, genetic variation in growth can have a component due to competing ability. As genetic improvement in competing ability is inevitably paralleled by a similar improvement in the mean competing ability of all contemporaries, there can be no net improvement in this trait. In this case, the prediction of response to selection for high growth rate is overestimated when calculated from the total additive genetic variance in the population.

Moav and Wohlfarth (1974) present a genetic model to describe this situation. The genetic value of an individual in a competitive environment is given as:

$$g + \alpha g + I$$

where

- g is the genetic value of the same individual in a non-competitive environment,
- α is a constant "magnifier" of this value (α can be negative) and
- I is a residual component due to "independent aggressiveness".

The regression slope of genetic value in a competitive environment on genetic value in a non-competitive environment is $1 + \alpha$, and I is independent from g. The total genetic variance in a competitive environment is thus:

$$(1+\alpha)^2 \mathrm{Var}(g) + \mathrm{Var}(I)$$

where

Var(g) is the total genetic variance in a non-competitive environment.

A parallel argument can be made considering additive genetic variance, giving

$$Var(a_c) = (1+\alpha')^2 Var(a_{nc}) + Var(I')$$

and

$$Var(a_{nc})$$

as the total additive genetic variance in competitive and non-competitive environments respectively.

The prediction of response to selection (R) by the standard formula,

$$R = ih^2\sigma_p$$

should use $h^2 = \dfrac{(1+\alpha')^2 Var(a_{nc})}{V_{p_c}}$ for competitive

environments, and

$$h^2 = \frac{Var(a_{nc})}{V_{p_{nc}}} \quad \text{for non-competitive}$$

environments, assuming that environments differ only in the competitive element.

Where fish are grouped in families for selection on family index, competition is only apparent within families and the additive genetic variance is greater within than between families. In this case, the within family index weight should be increased by a factor of $(1+\alpha')^2$, where the value of the additive genetic variance is calculated from a sib analysis in the normal manner.

Moav and Wohlfarth (1974) estimated α at unity for common carp under specified conditions. The genetic correlation between growth under competitive and non-competitive conditions was also estimated at unity.

It is considered that estimation of α' can only be carried out in a long term selection experiment under competitive and non-competitive conditions, or, where the basis of competition is clearly understood, by path coefficient analysis.

Griffing (1977) presents a comprehensive genetic model relating to this problem.

4. CROSSBREEDING

4.1. Interspecies crosses.

The literature indicates that artificial crossing can yield viable offspring in fish species of considerably distant relationship (Ayles, 1974; Kirpichnikov, 1969; Nygren *et al.*, 1972; Purdom, 1976; Refstie and Gjedrem, 1975), despite variation in chromosome number both between and within species (Scheel, 1966; Gjedrem *et al.*, 1977).

Refstie and Gjedrem (1975) have reported considerable, heterosis in 11 month weight of certain salmonid species crosses (table 4.1). Of note is the high growth rate of the Arctic char male x Atlantic salmon female cross. However, growth during the adult phase in sea water was not promising for species crosses (table 4.2), (Refstie, unpublished).

Table 4.1 Weights of salmonid hybrids at 11 months (grams) (Refstie and Gjedrem, 1975).

		Female parent			
		Char	Brown trout	Sea trout	Salmon
Male parent	Char	55.2	58.2	-	96.5
	Brown trout	73.3	41.8	-	7.7
	Sea trout	58.3	24.9	31.8	6.1
	Salmon	70.7	7.3	8.8	30.0

Table 4.2 Slaughter weight (kg at 4 years) of salmonid hybrids (Refstie, unpublished).

		Female parent			
		Char	Brown trout	Sea trout	Salmon
Male parent	Char	1.27	1.53	-	3.94
	Brown trout	2.07	1.93	-	2.26
	Sea trout	1.50	1.27	1.34	-
	Salmon	2.38	-	-	4.17

Although heterosis is evident in the char x salmon cross, the purebred Atlantic salmon had the better slaughter weight in the year class concerned. In two later year classes, this cross equalled, then was again inferior to the purebred salmon control. As any routine cross-breeding system requires the maintainance of pure species lines, the cross must be significantly superior to the best species available and thus the char x salmon cross is thought to be of no commercial value.

Heterosis for hatchability and survival in salmonid species crosses is usually zero or negative (Refstie and Gjedrem, 1975; Blanc and Chevassus, 1979; also see review by Chevassus, 1979). This can be due to poor synchronisation of maturity between species, but a general conclusion is that these traits cannot be improved by crossing salmonid species.

Ord et al. (1976) have shown partial dominance for resistance to Viral Haemorrhagic Septicaemia in a cross between Rainbow trout (susceptable) and Coho salmon (resistant). This approach to the development of disease resistant stock can be more practical than through selection. Ihssen (1973) has reported dominance of heat tolerance in a cross between Brook trout and Lake trout.

Marketing can be a major problem with interspecific hybrids. The plaice x flounder hybrid and the turbot x brill hybrid - both of which are easier to rear than their respective parents (Purdom, 1976) - have never been seen on the fishmonger's slab, and pose considerable marketing problems.

4.2. Interstrain crosses.

In a cross between two strains of Rainbow trout, Gall (1975) found heterotic effects on body weight at 2 years (+19%), number of eggs spawned (+9%) and egg size (-8%). However, Gjerde(1981b) found no signficant heterosis for slaughterweight in crosses of 5 Atlantic salmon strains. Wohlfarth et al. (1975b) present data indicating notable heterosis for growth in strain crosses of carp (table 4.3). However, the pure strain Dor-70 appears to perform about as well as the best strain cross.

Edwards and Gjedrem, (1979) have found considerable heterosis for tolerance to acid water in strain crosses of Brown trout. Survival of crossbreds to the alevin stage under acid conditions (pH 5.2) was double that of the pure strains (36% and 18% respectively).

Table 4.3 Corrected weight in grams of carp strains and strain crosses after a growth period starting at approximately 25 g.

		Female parent			
		Big belly	Nasice	Gold	Dor-70
	Big belly	345	515	486	523
Male	Nasice	-	475	600	597
parent	Gold	-	-	474	548
	Dor-70	-	-	-	594

4.3. Inbreeding and crossing.

There have been reports of inbreeding depression for many traits in various species. Moreover, sire x dam interaction has been found for several traits in family analyses. Crossing inbred lines has given rise to expected heterosis in carp (Moav and Wohlfarth, 1976) but little has been published with respect to crossing inbred lines of salmonids. Robinson et al. (1976) have reported dominance in tolerance to acid water in crosses between inbred lines of Brook trout.

Purdom (1969) has suggested that fast inbreeding with the aid of cytogenetic manipulations could prove to be central to the future development of farmed strains through inbreeding and crossing.

5. CYTOGENETIC MANIPULATIONS

The biology of fishes seems more buffered to withstand a change in ploidy (as indicated by Purdom 1972; Swarup, 1959; Valenti, 1975; Vasetskii, 1967), or somy at individual chromosomes (as indicated by Gjedrem et al., 1977) than most other higher animals. However, triploid individuals are almost invariably sterile (for example, Purdom, 1976) with poorly developed gonads. This phenonemon is highly desirable in the production of adult fish, as growth will not suffer the set-backs which are encountered in diploid fish at maturity: loss of appetite, reduced growth rate, lowered meat quality (Mills, 1970).

By subjecting fertilised eggs to cold shocks, Svardson (1945) produced one triploid embryo in 161 salmon x trout hybrid eggs which survived to the blastula stage. The first recorded success in producing adult triploid fish is in the stickleback (Swarup, 1959), by means of cold shocks. Subsequent growth of triploids did not differ significantly from their diploid sibs.

Purdom (1972b) reports a 100% success in the cold shock induction of triploidy in plaice and plaice x flounder hybrids. Triploid plaice have superior growth rates to their diploid contemporaries, and are sterile (Purdom, 1976). Valenti (1975) reports a 75% success rate in the cold shock induction of increased ploidy (triploids and tetraploids) in Tilapia aurea. At 14 weeks, polyploid fish were longer than their diploid sibs (polyploid 4.7 cm, diploid 3.5 cm, $P<5\%$).

Induction of triploidy in Atlantic salmon was not successful when cold shocks were used (Lincoln et al., 1974), but application of heat shocks has recently proved to be successful at a moderate rate (Refstie, personal

communication). Heat shock induction of triploidy in Rainbow trout has been reported by Chourrout (1980) and Thorgaard et al. (1981). It is generally believed that triploidy results from retention of the second polar body.

Tetraploid individuals are thought to have been induced in Rainbow trout and Atlantic salmon ((Refstie et al., 1977a, and Refstie, 1981, by use of cytochalasin B) and Rainbow trout (Thorgaard et al. 1981, by heat shock five hours after fertilization), through inhibition of the first cell division. Development of fertile tetraploid lines would facilitate the consistent production of triploids (from a tetraploid x diploid cross) without need for continuing treatments.

Alternative methods of producing sterile fish are by physical castration, by treatment with hormones (Johnston et al., 1978; Tayamen, 1978; Yamazaki, 1976), and by immuno - supression of the gonads (Chamberlain, 1978). These procedures can be expensive and are likely to be unacceptable in many countries.

Due to the low heritabilities for growth characteristics in common carp and flatfish, Moav (1965) and Purdom (1969) have suggested the formation of inbred lines followed by crossing, as practised by plant breeders. A rapid means of producing highly inbred individuals is by gynogenesis. Normal eggs are fertilised by radiation inactivated sperm, then subjected to cold shock treatment. The second polar body is retained, giving rise to diploid individuals. Due to crossing over in the oocyte at meiosis, these fish are not quite fully homozygous (Purdom, 1969).

Gynogenetic individuals have been produced in carp, sturgeon and loach (Romashov et al., 1961), plaice and flounder (Purdom, 1969), Rainbow trout (Purdom, 1969, and Chourrout, 1980), Coho salmon and Atlantic salmon (Refstie personal communication). Heat shock was used in the case of Atlantic salmon. However, these individuals have usually died at an early stage, or suffered other effects of inbreeding depression. Use of partially inbred stocks, in which the frequencies of deleterious recessive genes has been reduced, might serve to increase viability following gynogenesis.

6. PRESERVATION OF GAMETES

Frozen semen of Rainbow trout and Atlantic salmon is becoming involved in experimental breeding work following the partial successes of Buyukhatipoglu and Holtz (1978) and further improvement (up to 80% of control fertilization rate) by Stoss and Holtz (1981).

A major application of this technology is to help generate reference control populations in selection work. Random bred control populations are subject to considerable unintentional selection, especially in those species which are recently domesticated. However, contemporary use of batches of semen generated and stored in different years can give an unbiassed estimate of selection response. Repeat mating employing storage of semen can also give an estimate of selection response, but this is complicated by selection bias and other factors.

Erdahl and Graham (1980) have stored fertilised Brown trout eggs for an unstated period at -20°C with an 88% rate of survival. Further success in this field could give rise to the cryopreservation of whole control populations.

7. DISCUSSION

The present scope for genetic improvement of fish seems to be favourable in comparison to that for domestic mammals and poultry. Most traits are more variable in fish species and selection intensities can be very high. In most cases, these two factors more than compensate for the generally lower heritabilities which have been found. Moreover, the additional value of using family information in selection indices is greater in fish because of these lower heritabilities and the large family sizes involved.

Slaughter weight in fish is usually of major economic importance - wholesale prices being linked to fish weight. In salmonids, response to family index selection for this trait is expected to be over 3 percent per year. Although little breeding work has been carried out with other recently domesticated species, it seems reasonable to speculate that response to selection will also be high for these. However, selection over five generations failed to improve growth rate in carp (Moav and Wohlfarth, 1976). This is attributed to a long history of mass selection causing the population to reach a plateau.

Developments in the technique of gynogenesis and sex reversal will aid in the fast production of inbred lines for inbreeding and crossing programs. Such programs are common in plant breeding, but they have failed in animal breeding due to unviability of inbred individuals and the time required to establish inbred lines. An area of great need here is to study the variance between crosses of inbred lines - this parameter is central to the practical value of such breeding programs.

Genetic improvement of the shellfish species is a subject which deserves more attention than it receives. Kirk (1979) estimates that molluscs form 98% by weight of all marine species cultured in the European Economic Community. Manson (1973) reports that culture of the mussel Mytilus edulis linneaeus on ropes in Spain can realise a yield of 120 tonnes per hectare per year of edible flesh, without any artificial feeding. This must be one of the most biologically efficient meat production systems in existence.

Moav et al. (1978) outline a scheme for the genetic improvement of wild fish stocks, and Kinghorn (1980b) has developed a computer program to predict the most cost efficient approach to such a scheme. Release of fry of domestic salmonids and carp is widely practised, but their performance in the wild has usually been inferior (Flick and Webster, 1976). Moav et al. propose the crossing of wild fish strains with domesticated breeds in a program designed to upgrade wild stocks. Progress in such a program could be monitored with the aid of polymorphic gene markers.

With the increasing interest in "ocean ranching" (release of juvenile fish which return as adults to the river of origin), more attention is being focused on genetic parameters of traits such as migratory behaviour, growth in the wild and return frequency (Saunders and Bailey, 1980). Traits even less familiar to the quantitative geneticist may become important in the future if the large open sea mariculture units which are forecast become a reality (see Hanson, 1975). Genetic improvement of the efficiency of such a system could involve more than one species with complications due to interaction between species. This would require an extension of current animal breeding theories.

PART III

GENETIC VARIATION IN FOOD CONVERSION EFFICIENCY AND GROWTH IN RAINBOW TROUT

PART III

GENETIC VARIATION IN FOOD CONVERSION EFFICIENCY AND GROWTH IN RAINBOW TROUT

1. INTRODUCTION

The main aim of this experimental project was to study genetic variation in food conversion efficiency and growth in Rainbow trout (Salmo gairdneri). This species was chosen because it is of major importance in Europe and North America, and because it is more tolerant to stress caused by experimental handling than the other species which was available, Atlantic salmon (Salmo salar).

This type of work has not previously been undertaken because of the difficulty in measuring directly the food consumption of a sufficiently large number of fish to estimate genetic parameters with reasonable accuracy.

Under commercial conditions, fish will not eat all the food they are offered, and uneaten food is generally mixed with faecal material on the bottom of the tank or pond - making impossible the measurement of food consumed.

Some researchers have made use of floating pellets and others have hand fed to appetite with close observation to see that all food offered is consumed. However, these techniques were rejected because of the very high labour costs involved and significant environmental deviations from commercial conditions.

Skjervold (1979, personal communication) proposed the concept of using metabolic rates, estimated via oxygen consumption, to help provide estimates of food consumed.

2. AN INDIRECT ESTIMATE OF FOOD CONSUMPTION

Figure 3.1 describes the energy budget of a fish. The gross energy in food consumed over a period of time can be partitioned:

$$E_{fc} = E_f + E_m + E_n + E_d$$

Knowing the energy digestibility of the diet for the fish concerned,

$$dg_e = \frac{E_a}{E_{fc}} \quad \text{, this can also be given as:}$$

$$E_{fc} = \frac{(E_m + E_n + E_d)}{dg_e} \qquad (2.1)$$

E_m can be estimated through a knowledge of oxygen consumed, (see, for example, Brody, 1945; Warren and Davis, 1967; and Brett and Groves, 1979). Brody (1945) gives the constant 3.5 calories per mg oxygen consumed, but this can vary according to the type of nutrient metabolised. Brett and Groves (1979) quote separate constants for protein (3.20), carbohydrate (3.53) and fat (3.28) which are derived from theoretical considerations of the biochemistry of metabolism in fish.

Knowing the proportions of these nutrient classes metabolised, a weighted mean constant can be calculated. A full treatment of this problem will involve measurement of the digestibility of each nutrient class and a consideration of the nutrient components of deposited tissues in order to estimate the proportions of each nutrient class actually metabolised. However, as the three constants given by Brett and Groves (1979) do not vary greatly, use of the proportions of each nutrient class in the diet fed will yield a reasonable approximation. For the diet used in this project (40% protein, 35% fat, 25% carbohydrate), the constant is 3.31 calories per mg oxygen consumed.

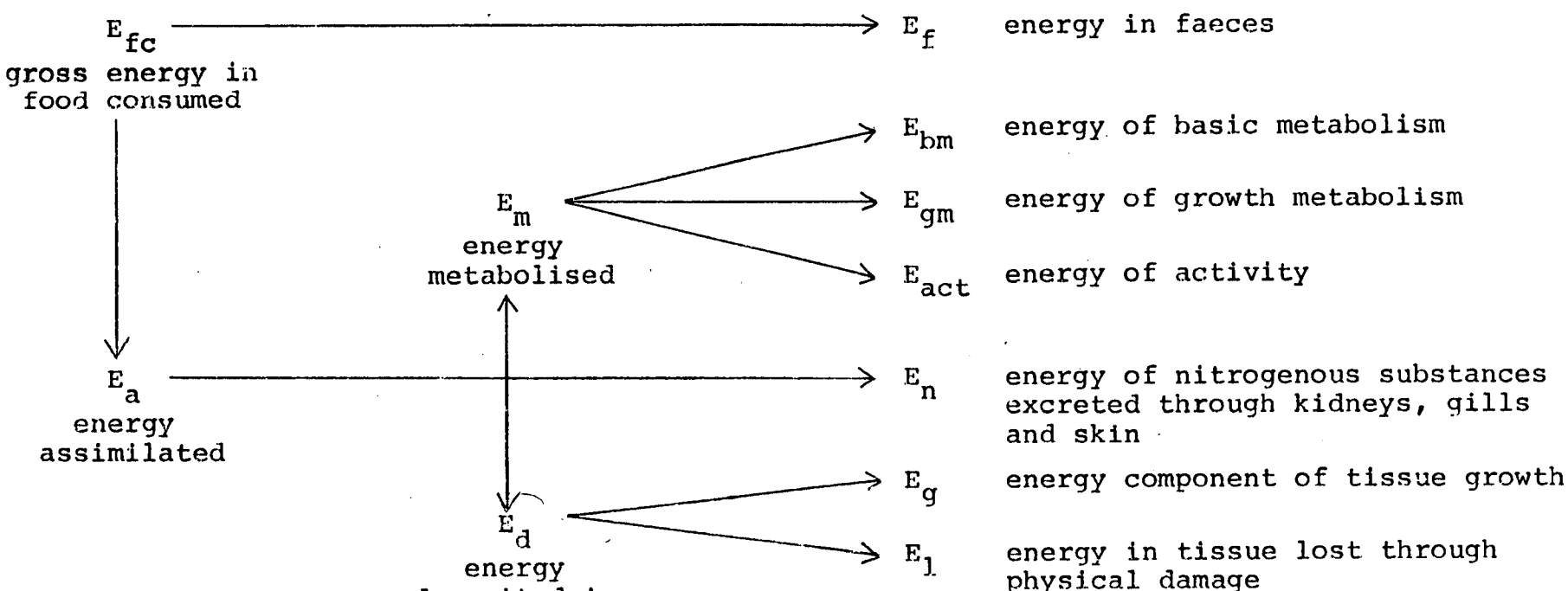

Figure 3.1. The energy budget of a fish.

E_n is difficult to measure (see, for example, Post et al., 1965) and this would involve unreasonable expense in genetic work where many measurements are required. However, E_n is expected to be small. Smith et al. (1978) state that 85% of waste nitrogen is excreted as ammonia, which possesses no biological energy value. E_n has been estimated at 7% (Winberg, 1956) and 8% (Cho et al. (1976) of the gross energy value of the food consumed. Accordingly, $E_n = 0.075E_{fc}$ is assumed hereafter.

E_d is estimated by E_g under the assumption that tissue loss through physical damage is negligible. From equation 3.1, E_{fc} can be given as:

$$E_{fc} = \frac{(k_1 O_2 cons + 0.075E_{fc} + E_g)}{dg_e}$$

$$E_{fc} = \frac{k_1 O_2 cons + E_g}{dg_e - 0.075} \qquad (2.2)$$

where k_1 is calories metabolised per mg oxygen consumed (O_2cons). Grams food consumed (FC) is estimated by:

$$FC = \frac{E_{fc}}{k_2}$$

where k_2 is the amount of calories per gram of feed. Alternatively, a valid estimate of the metabolisable energy of the feed (ME, cal/gm) can be utilised.

$$ME = \frac{E_a - E_n}{FC}$$

$$FC = \frac{E_m + E_d}{ME}$$

$$FC = \frac{k_1 O_2 \text{ cons} + E_g}{ME} \qquad (2.3)$$

Following this approach, energy digestibility is assumed to be the same for each fish or group of fish.

3. MATERIALS AND METHODS

3.1. An overview.

The experimental work was carried out at the Research Station for Salmonids, Sunndalsøra, Norway, utilising the two year classes of Rainbow trout which hatched in the springs of 1979 and 1980.

For one year after hatching the trout are reared in fresh water tanks at Sunndalsøra. They are then transferred to sea water net cages at another site. As the recording of oxygen consumption required the development and use of special facilities, it was necessary that the experimental work be carried out at Sunndalsøra during the fresh water period. Under this restriction, the end of the fresh water period was chosen as representing the growth phase of most commercial relevence.

The trout are unmarked at this stage and, to retain family identity, each full sib group is reared separately in its own tank. 145 families were available to the project over the two year classes.

To measure the oxygen consumption of each fish is totally impractical on this scale, involving unreasonable capital and labour costs, and very large deviations from commercial rearing conditions. Accordingly, these measurements

were made on full sib groups, as were all other measurements in the experiment. The following were recorded for all groups (or replicates):

1) Total group weight at the beginning and end of a growth period of 3-4 weeks.
2) Oxygen consumed over this period.
3) Food delivered into the tank during this period.
4) Number of fish in the group.
5) Number and weights of mortalities during this period.

For some groups the following were also recorded:

6) Nitrogen digestibility of the diet. (66 groups and replicates).
7) Energy digestibility of the diet. (15 groups and replicates).
8) From samples of 5-10 fish taken at the beginning and end of this period, (66 groups and replicates):
   a) % nitrogen
   b) % dry matter
   c) % ash
   d) energy concentration (cal/gm fish)

The oxygen recording equipment developed for the project monitors 33 tanks in any one growth period or "run". Seven runs were completed over the two seasons of experimental work, giving a total of 231 tank-runs. This comprised 145 full sib families plus 86 replicates, both within and between runs. Table 3.1. gives some basic information about each of the seven runs.

At the beginning of each run, all groups of fish were reduced to a total weight of about 5 kg per tank by random rejection. Families were allocated to run in a stratified random manner, ensuring, as far as possible, that each run included at least one family of each of the sires involved in the year-class. Families were allocated to tanks within

Table 3.1. Some basic information about each of the seven experimental runs. Water temperature was measured three times daily. Mean weight of fish is given as the average of the tank means.

Run	Date started	Data ended	Mean water temp. (°C)	Mean weight at start (g)
1	24.12.79	1.1.80	7.4	40.1
2	1.1.80	28.1.80	9.2	42.3
3	4.2.80	26.2.80	11.9	74.9
4	28.2.80	22.3.80	10.7	88.0
5	1.12.80	5.1.81	8.1	31.1
6	6.1.81	2.2.81	9.5	38.4
7	2.2.81	2.3.81	11.5	51.8

runs in a random manner, with the exception that replicates between runs retained the same tank in order not to confound run effects and tank effects.

Run 1 was terminated after 8 days in order to make a modification to the automatic feeders. This period was considered to be unacceptably short, and so the stock from run 1 was retained for use in run 2, each group remaining in the same tank.

The 1979 year-class involved only 13 sires - a consequence of the high intensity of selection in the population. Selection was relaxed the following year to give 21 sires of the 1980 year-class. No sire or dam was represented in both year classes.

3.2. Measurement of oxygen consumption.

The system developed to measure oxygen consumption is based on fry tanks (surface area 1 m^2, water depth 25 cm) which are standard equipment at Sunndalsøra. Water is not recirculated. In a through-flow system, rate of oxygen consumption (mg O_2/min) is the product of:

i) the reduction in dissolved oxygen concentration (mg O_2/liter) between inlet (fresh) water and outlet (used) water.

ii) the rate of flow of water (liters/min) through the tank.

A cover should be placed on the tank to prevent oxygen transfer across the surface of the water - any such transfer is not accounted for in the above consideration.

3.2.1. Recording of dissolved oxygen concentration (DOC).

The following objectives were involved in the development of a system to measure and record DOC's:

1) Measurements should be continuous or frequent in order to cover any fluctuations in oxygen consumption. This obviated the possibility of using manual titration techniques, and dictated the use of an oxygen metering device which can give a continuous DOC reading.

2) In view of the large number of recordings envisaged, all data should be directly stored on magnetic tape.

3) The experimental error and bias should be minimal. Trials with a Yellow Springs Instruments model 57 oxygen meter and matching probe no. YSI 5739 showed that readings would be typically 5% in error after a period of four days from calibration. This caused the rejection of an early proposal to use one probe at the outlet of each tank plus 3-5 probes in the inlet water supply.

Following these objectives, a system was designed comprising the following (with reference to figures 3.3 and 3.4):

a) Water samples (35 in total) flow by gravity from the tank outlets (33 samples) and from the water inlet source (2 samples) to the system in 10 mm clear polyvinyl chloride (PVC) tubing.

b) A water sampler diverts one water sample at a time to the measuring equipment.

c) Sampled water passes over oxygen probe, type YSI 5739.

d) A YSI model 57 meter displays DOC.

e) Reference information from photocells in the water sampler is transmitted to a data compiler.

f) The data compiler coordinates information from the water sampler and the oxygen meter.

Figure 3.2. An overview of the experiment during the 1979/80 season. The central red pipe supplies inlet water. The water flow controllers are mounted adjacent to this pipe, one per tank. The green tubes carry overflow water from the controllers. The top halves of the automatic feeders are protruding from the plastic covers. Each tank's central drain leads to a black waste pipe, one pipe per row.

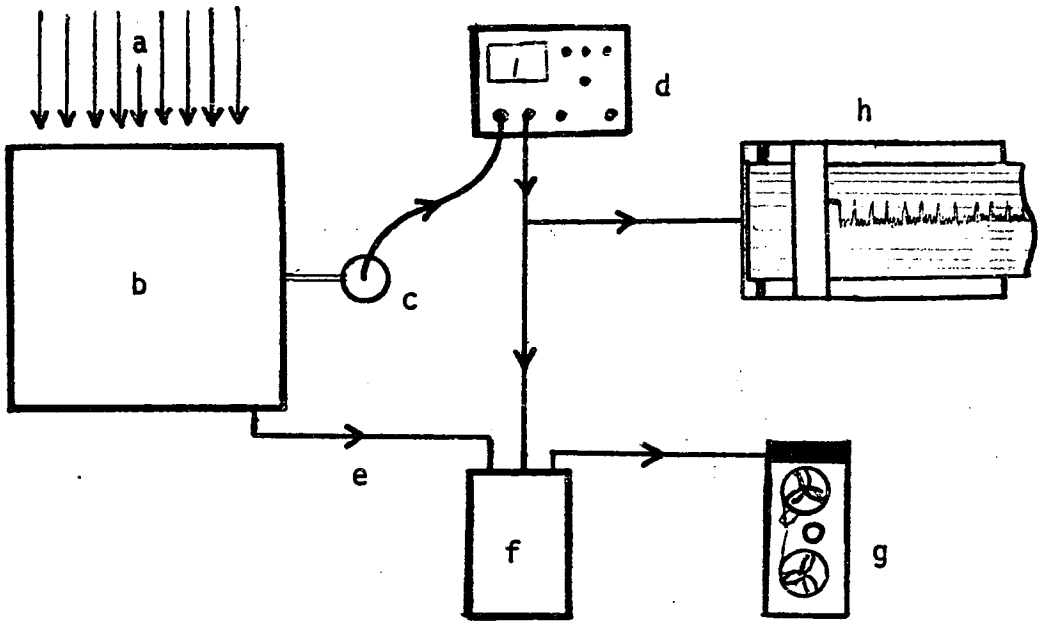

Figure 3.3. Diagram of system.
Arrows indicate flow of information. a - water samples from water supply and tank outlets. b - water sampler. c - oxygen probe. d - dissolved oxygen meter. e - reference information from photocells. f - data compiler. g - data logger, magnetic tape. h - pen recorder, for visual monitoring of the system.

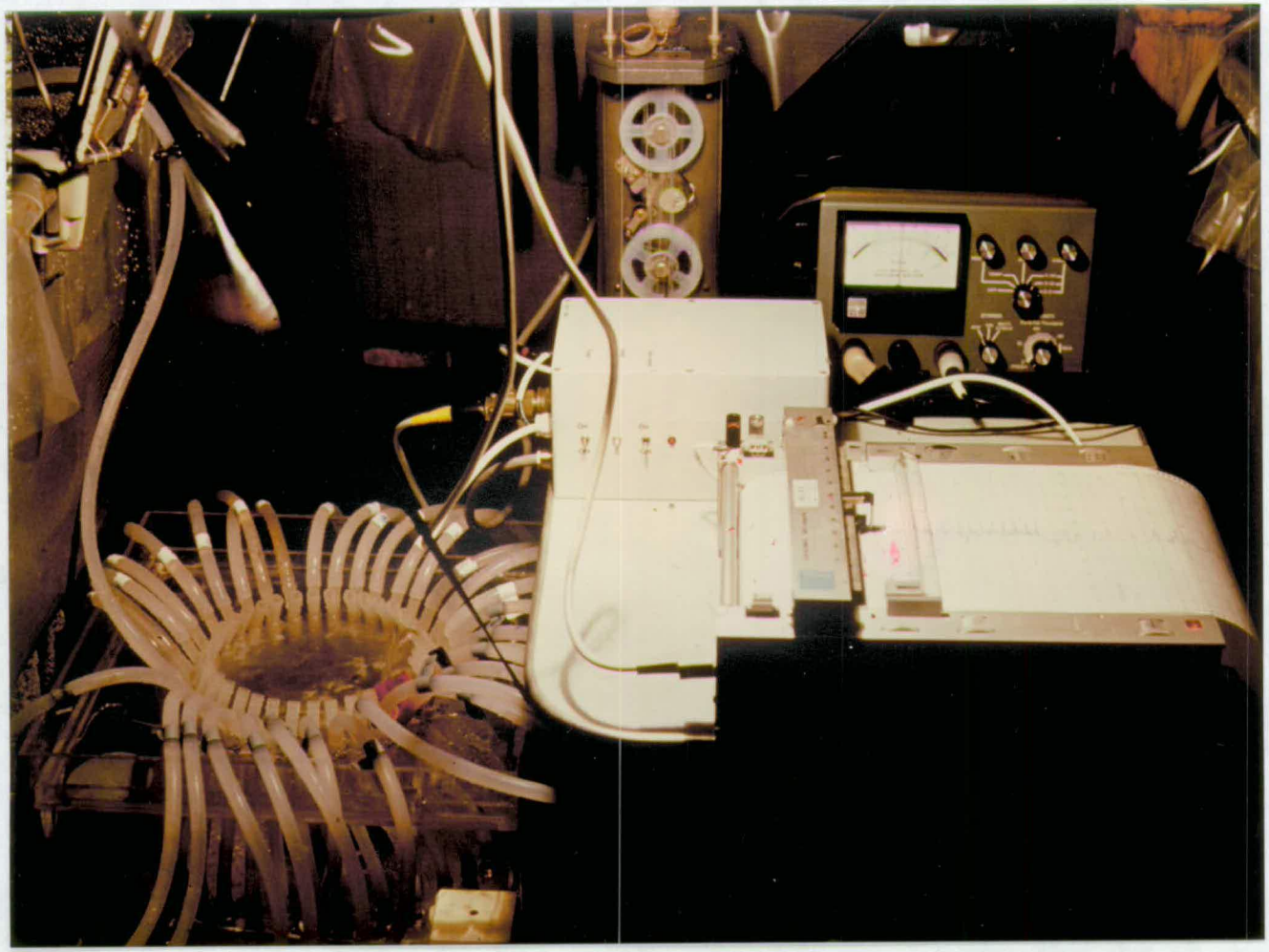

Figure 3.4. The water sampler and recording equipment situated in the space vacated by the middle tank of the left hand row (Figure 3.2). Description of components follows figure 3.3.

g) A data logger records reference information and DOC on magnetic tape.

h) A pen recorder displays DOC at each source over the previous few hours.

The water sampler (figures 3.5 - 3.11) is a perspex box with 35 input tubes carrying water from 33 tank outlets and from the water supply pipe (2 tubes). At any one time, one sample of water is carried to the oxygen probe and the remaining 34 go to waste.

With reference to figures 3.5 and 3.6, each input tube is connected at the top of the sampler (level 1, figure 3.5) to a Y junction (3) with one end open. Excess pressure is released by overflow at this open end such that the water flow rate over the oxygen probe (11) is equal for each of the sampler's 35 "channels". This is necessary because the oxygen probe's operation is based on a chemical reaction which is limited by the rate of passage of oxygen molecules through a teflon membrane into the probe. The rate of this oxygen consumption by the probe itself is sufficient to appreciably deoxygenate the sampled water. Thus, oxygen readings are positively correlated with flow rate and a standardisation of flow rate is required.

Flow from the channel currently being sampled is diverted at an intermediate level (level 2, figure 3.5) by the pick up arm (7) and led to the oxygen probe via a swivel join (figure 3.5, 20). Water from all other channels drops freely from level II to the bottom level (level 3, figure 3.5), from where it flows to waste drain pipe (15). The pick up arm (7) is mounted on a ratchet cog wheel (8) which is activated once every minute to move the pick up arm to the next channel.

A photocell (figure 3.5, 18) mounted at the 1 rpm motor which drives the ratchet (figure 3.5, 17), activates the

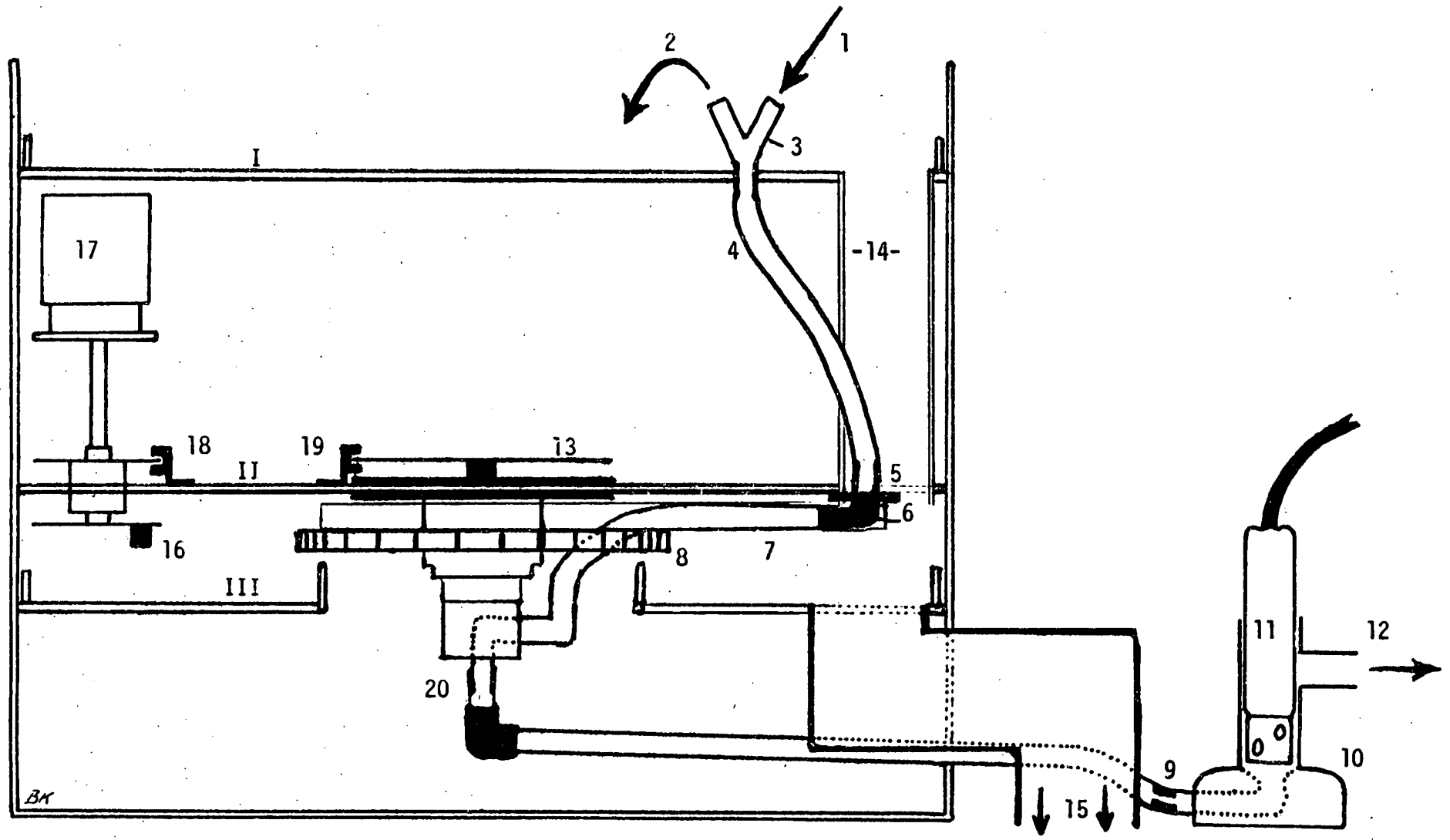
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Figure 3.5. Water sampling machine - side view. (opposite). Arrows indicate flow of water. Only one of the 35 channels is shown (that currently being sampled) and the ratchet mechanism is not shown. I - level 1, II - level 2, III - level 3. 1 - input of sampled water via 10 mm tubing. 2 - overflow due to backpressure from restrictor (9). (3 to 16 are in common with figure 3.6 3 - Y-junction, one per channel. 4 - connection tube. 5 - brass connector, from here water falls to level 3 or is diverted if currently sampled. 6 - collection cup, this is sprung upwards to form a seal against the perspex sheet of level 2, outward leakage is negligible. 7 - pick-up arm. 8 - 35 tooth cog wheel, this carries the pick-up arm. 9 - restrictor, this is adjusted such that the channel with the lowest input pressure just overflows at 2, ensuring the same flow rate over the oxygen probe for each channel. 10 - probe holder, sampled water is diverted upwards for immediate contact with the oxygen sensor of the probe. 11 - oxygen probe. 12 - sampled water to drain or other measuring equipment. 13 - rev. counter plate with gap to activate photocell (19). 14 - drain from level 1 to level 3. 15 - drain from level 3 to disposal. 16 - ratchet drive plate with offset pin. 17 - electric motor, 24v. a.c., 1 r.p.m. 18 - photocell, activated by plate with gap as in 13, initiates recording of oxygen level for sampled channel just before movement of the pick-up arm. 19 - photocell, stimulates electronic counter once for every full turn of the pick-up arm. 20 - swivel join, PVC tube over stainless steel tube, silicon lubricant, no leakage.
The size of the machine is approximately 41 cm x 41 cm x 38 cm including the probe holder and waste drain 15.

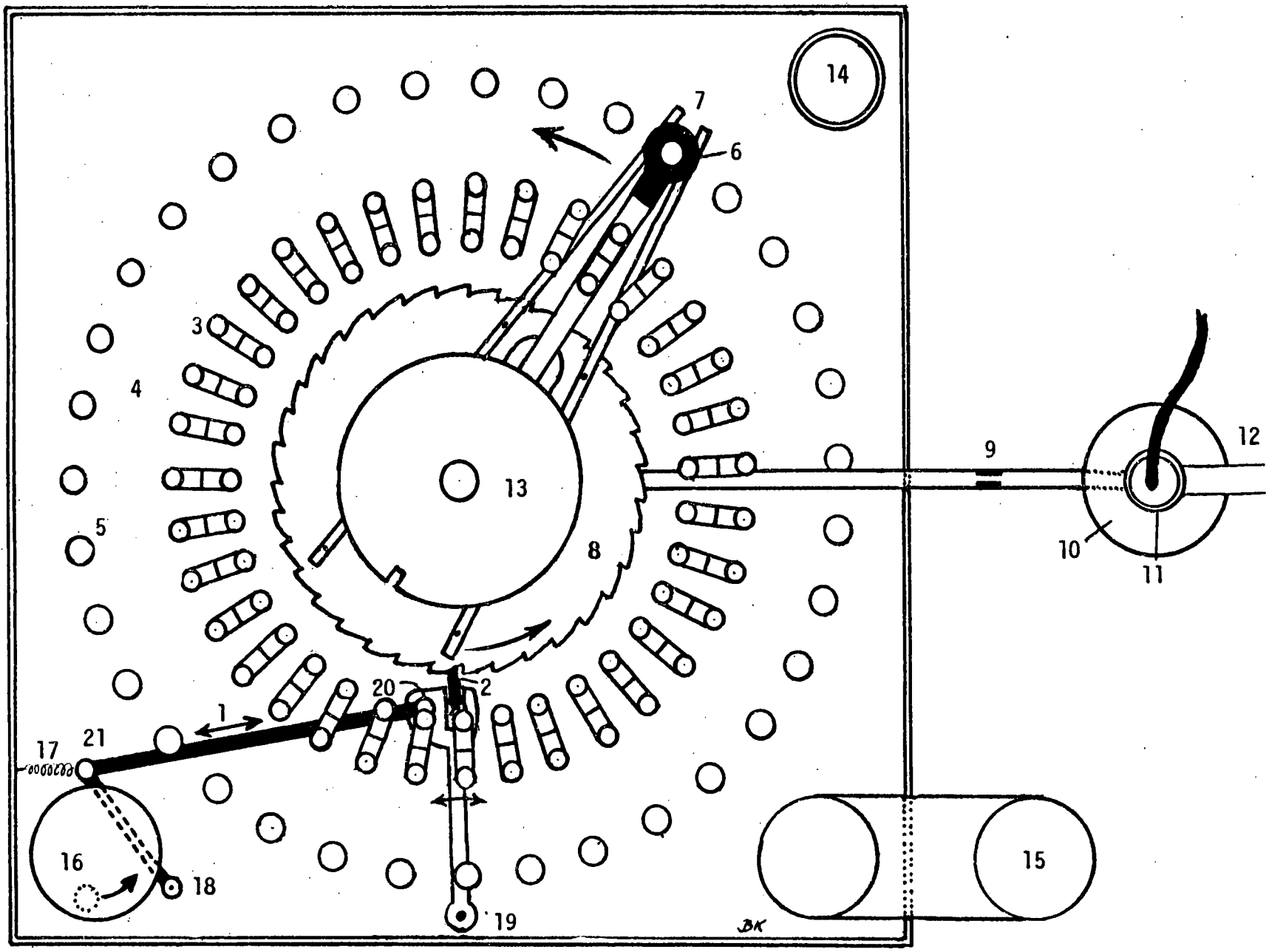
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Figure 3.6. Water sampling machine - top view. (opposite) Arrows indicate mechanical motion. The motor, photocells and all but one connection tube (4) are not shown. 1 - ratchet mechanism, this is activated by an offset pin (16) once for every full turn of the motor, causing the pick-up arm to move anti-clockwise to the next channel. 2 - sprung ratchet tooth. 3 to 16 as in figure 3.5. 17 - ratchet return spring. 18 and 19 - pivot points. 20 and 21 - flexible joints.

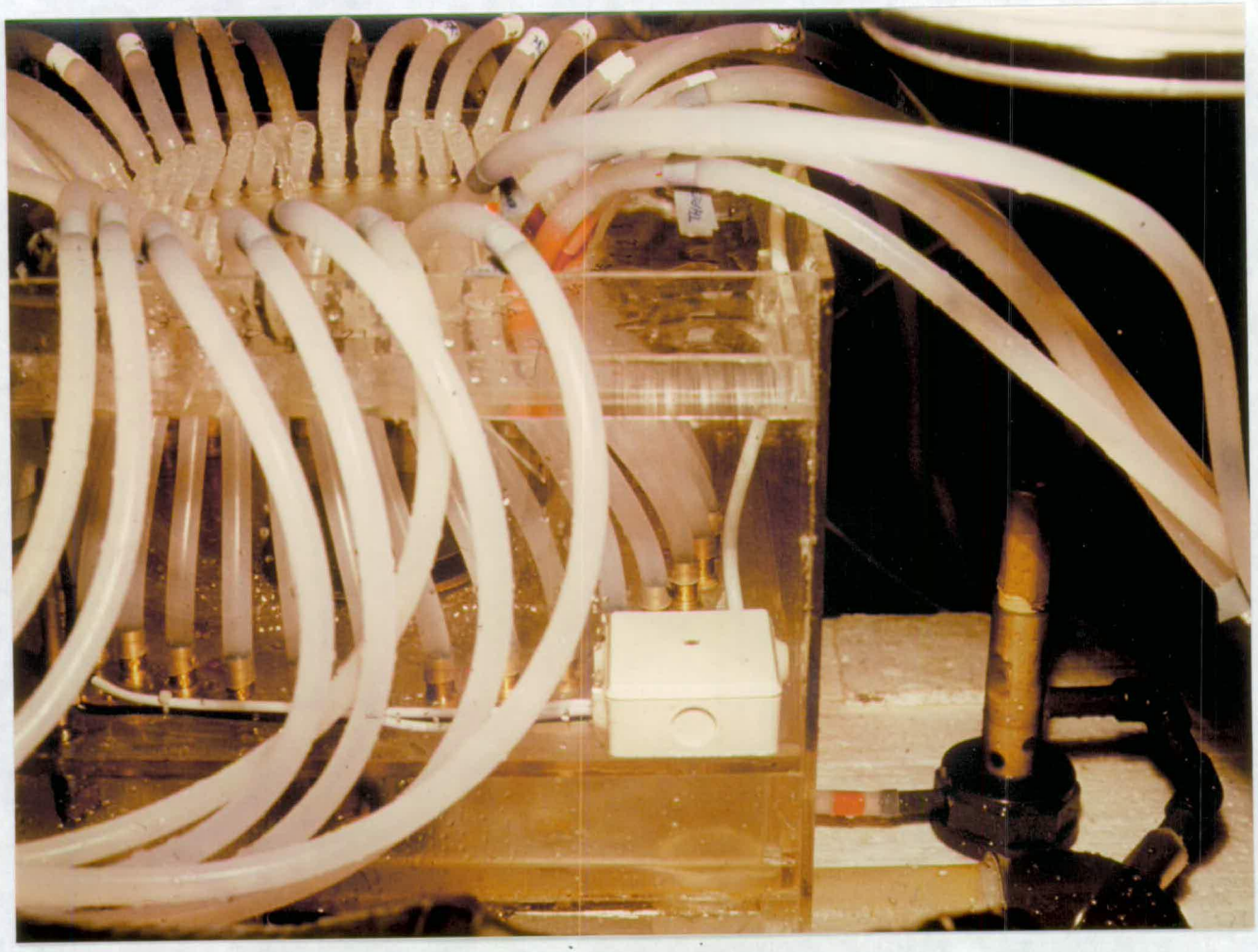

Figure 3.7. The water sampler and the oxygen probe in its holder. Orientation is as figure 3.5.

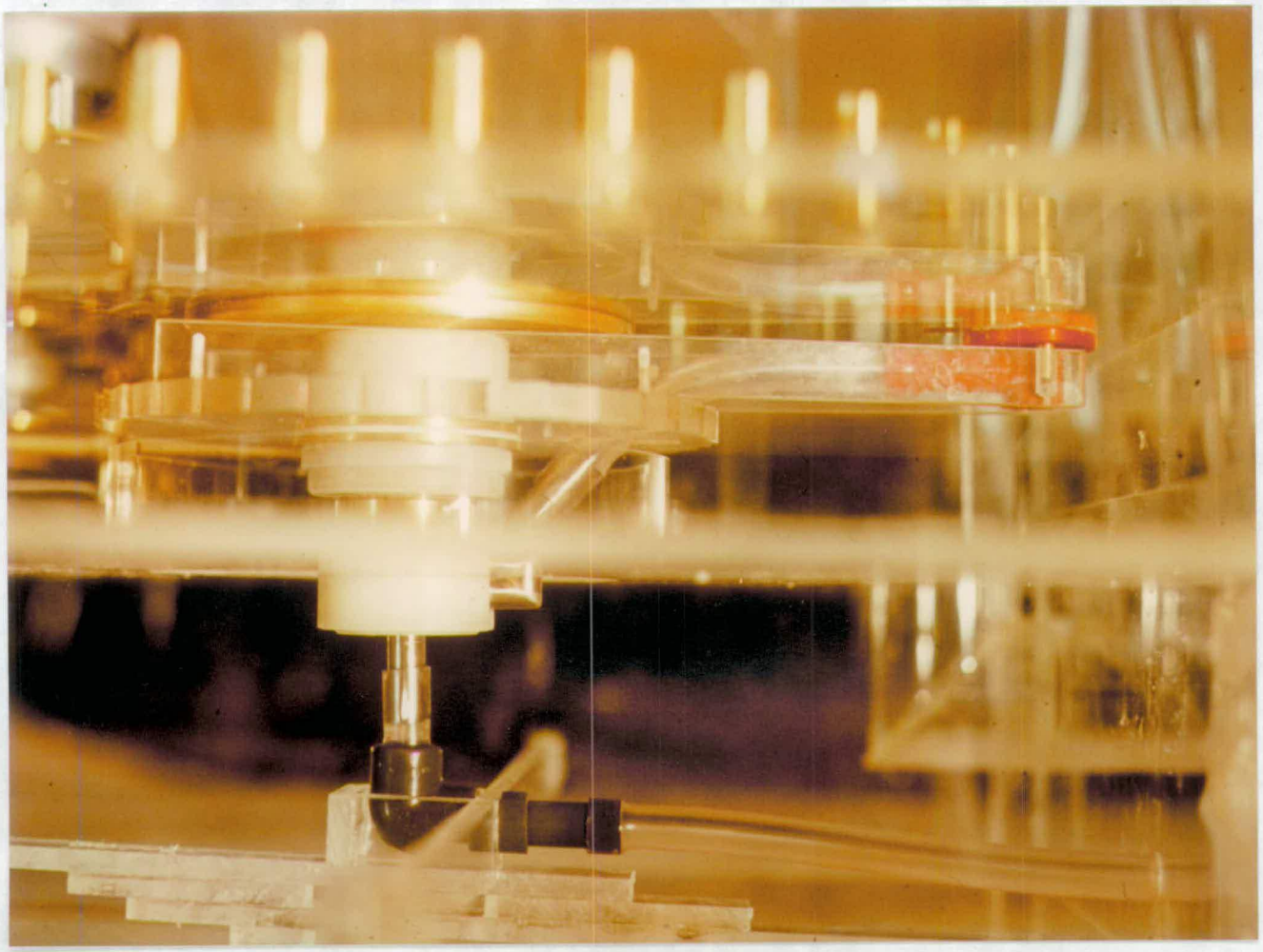

Figure 3.8. The pick up arm of the water sampler. The red PVC cup is sprung against the perspex sheet of level 2 to give a leak-free collection of sampled water.

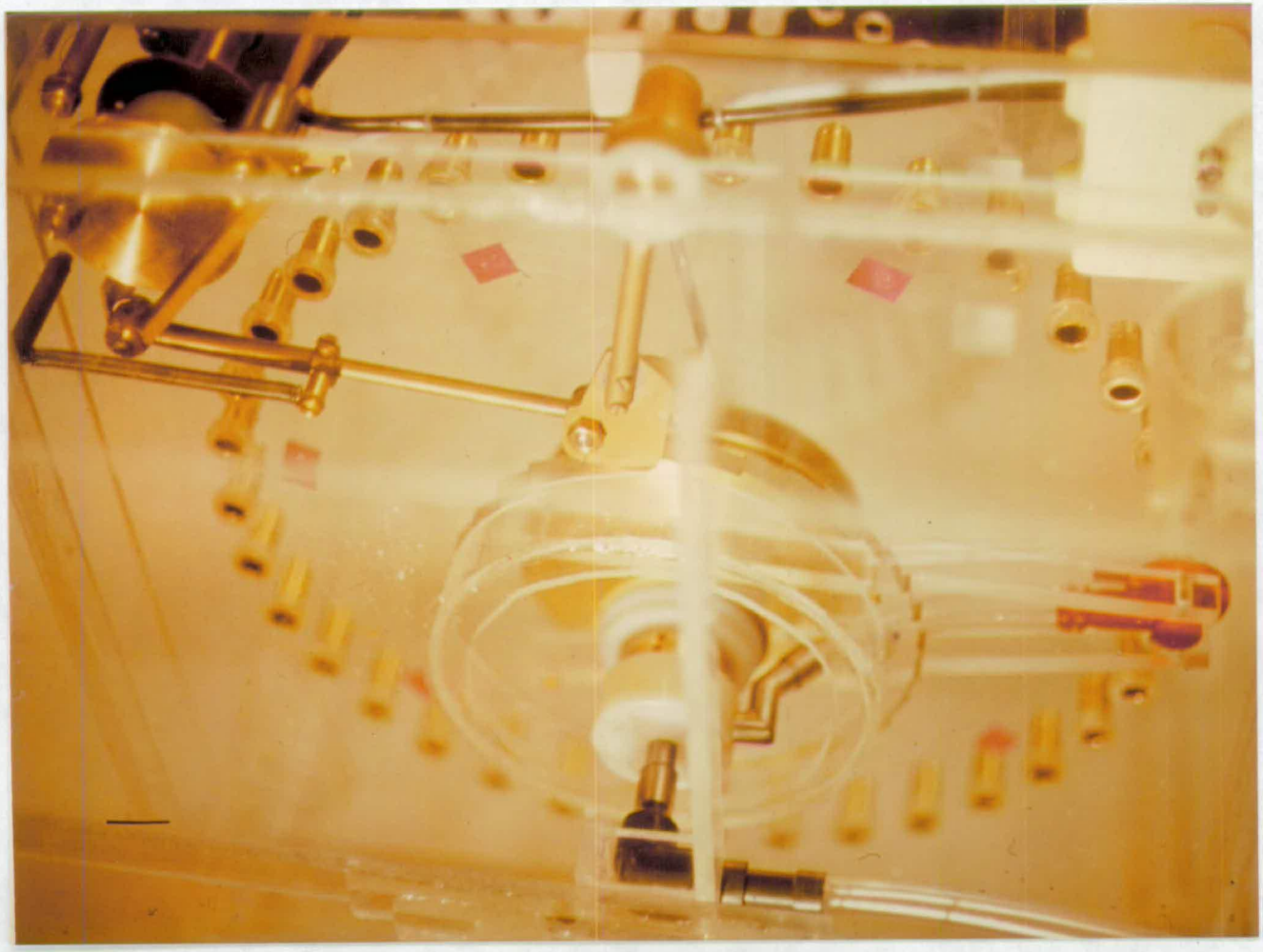

Figure 3.9. The ratchet mechanism of the water sampler. The operation of this mechanism is illustrated in figure 3.6.

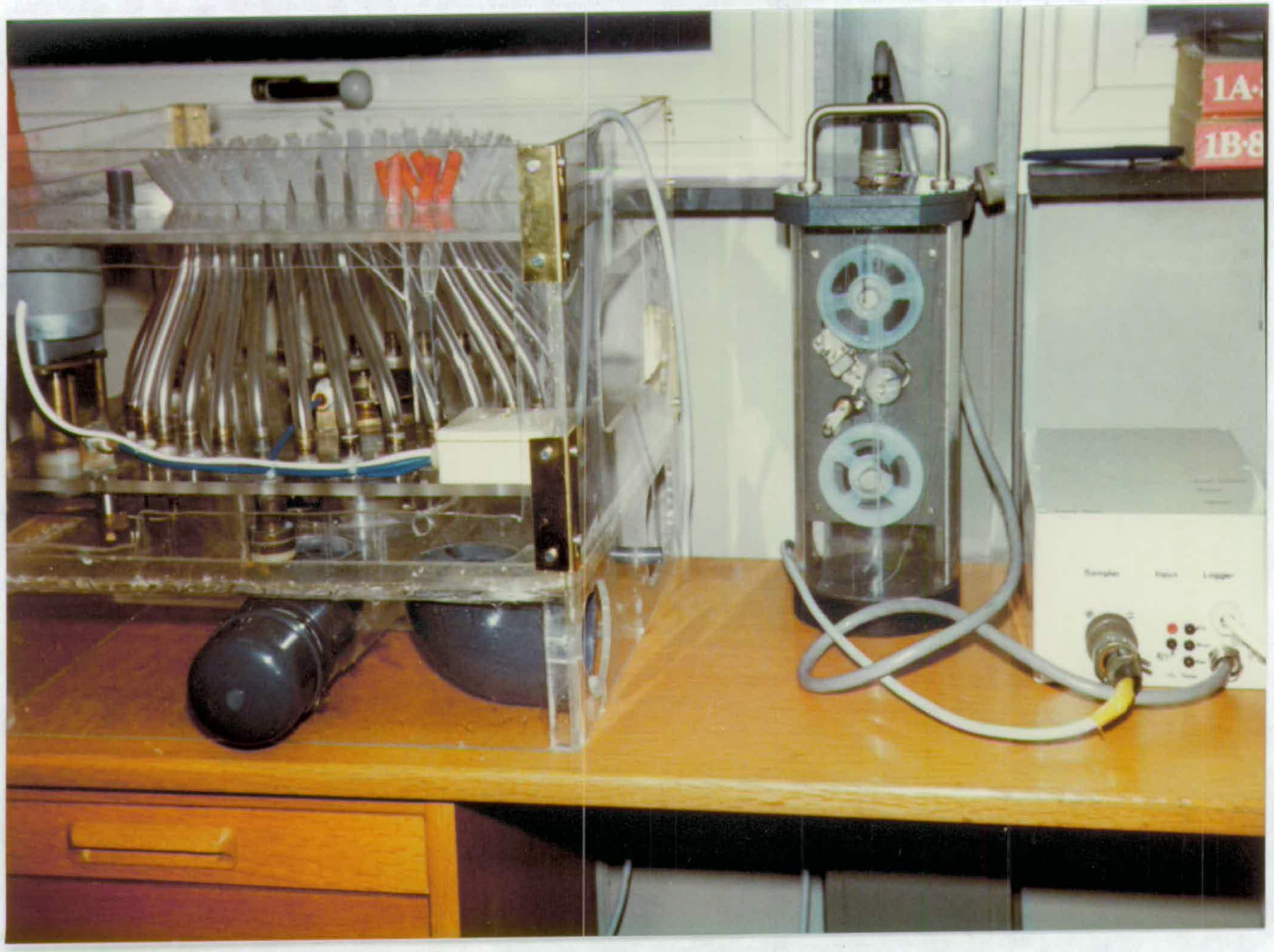

Figure 3.10. The water sampler, data logger and data compiler.

Figure 3.11. Setting up the experiment in December 1979. This photograph illustrates how levels 1 and 2 of the water sampler can be lifted out for repair or maintainance.

recording equipment just as the pick up arm moves to the next channel. The measuring equipment has one minute to equilibrate at each channel before a reading is taken.

A second photocell (figure 3.5, 19) activates a counter circuit in the data compiler (figure 3.3, f) which stores a record of the number of full turns of the pick up arm. This information is recorded on magnetic tape in addition to DOC readings.

Level 2 of the water sampler and the components mounted directly thereon were constructed to specifications by Mr. R. Markussen and staff of the Institute of Physics at The Agricultural University of Norway.

The water sampler and other equipment shown in figure 3.4 were positioned in the space vacated by one 1 m^2 tank. The 33 tanks were set in two rows (figure 3.2), 17 in one row and 16 tanks plus one space at half way in the second row.

With no fish in the tanks, the coefficient of variation of DOC between channels was approximately 0.002, indicating a very low equipment bias between tanks despite the range in length of input sample tube (1 m to 12 m) between each tank outlet and the water sampler. The oxygen consumption of the fish food itself was shown to be negligible by its lack of effect on DOC of water in tanks with no fish present (see figure 3.12).

The following problems were encountered over the two seasons when the system was in use:

1) The hub which carries the pick up arm and cog wheel (figure 3.5, 7 and 8) seized on four occasions in the 1979/80 season. This effect could not be simulated outside the fish hall, and was considered to be due to a combination of humid conditions and accumulation of

foreign material. Increasing the tolerances around the hub reduced the problem to two seizures during the 1980/81 runs. A sealed roller bearing was then installed. This should eliminate the problem in future use of the sampler.

2) Stimulation of photocell 18, figure 3.4, would at times affect the oxygen meter reading. This was caused by a conduction of electrical charge over wet surfaces and bodies of water to the probe sensing mechanism. Use of a silicone based spray would temporarily cure this problem. Before the 1980/81 season, the two photocells were replaced by electromagnetic transducers which do not cause this type of problem.

3) The 10 mm PVC tubes which carry water to the sampler from the tanks can accumulate uneaten food and faecal material which can eventually cause a blockage. This problem is reduced by minimising overfeeding. The tubes were either blown out using compressed air or cleaned with a long piece of PVC wire at least once per week.

A pen recorder (figure 3.3, h) was included in the system to act as a visual monitor. Example traces from this recorder are given in figure 3.12.

3.2.2. Control of water flow rate.

A flow controller was developed which has proved more accurate than commercially available flow meters. A major advantage in this controller is that any predetermined flow rate can be maintained, enabling a degree of environmental manipulation to eliminate differences between tanks.

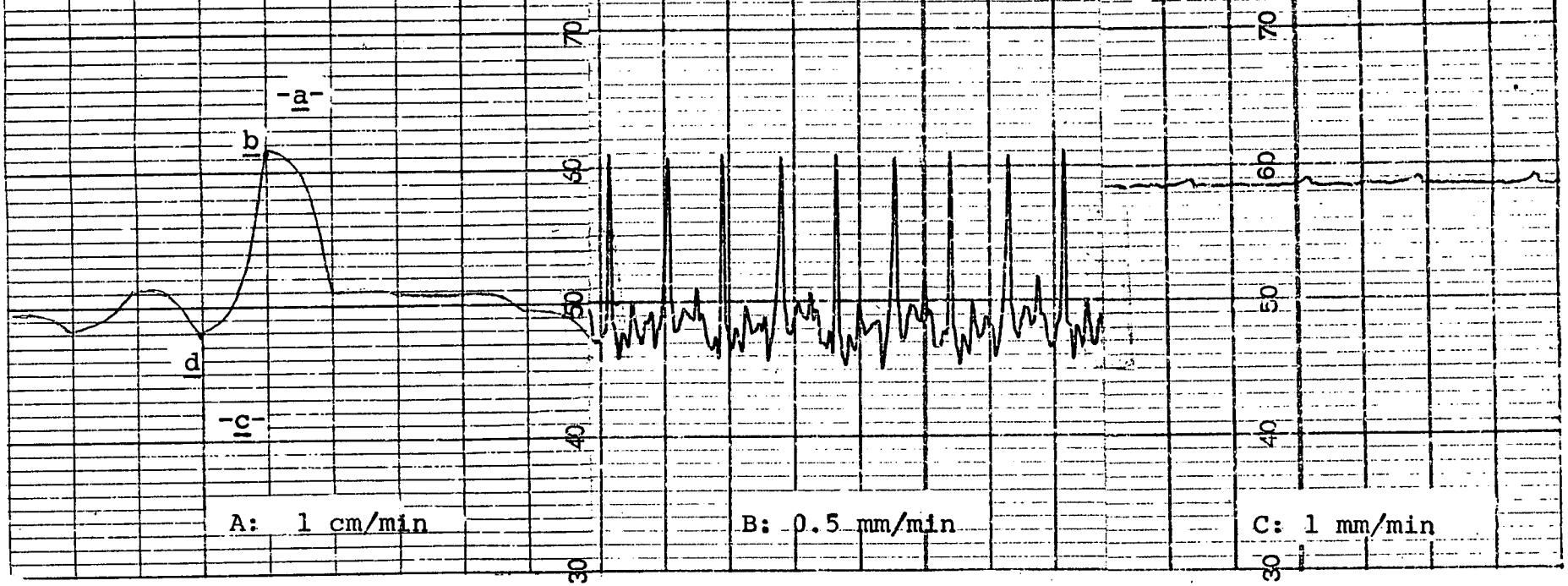

Figure 3.12. Sample traces from the pen recorder - DOC (mg O_2/liter x 5). The pen moves leftwards in relation to the paper.

A: This trace illustrates the nature of the response of the oxygen probe to a change in water source. During period a, inlet (high DOC) water passes over the probe. At time b the equilibrated DOC of this water is reached (about 95% response in one minute) and recorded by the data logger. During period c water from the outlet (low DOC) of one tank passes over the probe and the equilibium DOC is recorded at time d, and so on.

B: High peaks represent inlet samples (2 per 35 minute cycle) and low levels between these peaks represent outlet samples (33 per 35 minute cycle).

C: No fish in the tanks. The small peaks representing inlet samples are due to the significantly higher pressure of these samples. This is not fully stabilised by level 1 of the water sampler (figure 3.5). This trace was not notably affected by introducing a large handfull of fish food into every second tank - indicating that the food itself does not consume a signficiant quantity of oxygen.

Differences between traces in inlet sample DOC's is due mainly to differences in water temperature.

Construction is based on polyvinyl chloride (PVC) components throughout. 0.5 meter of clear tubing (63 mm outside diameter, 3 mm wall thickness) is blanked off at one end to form a vertical cistern which is mounted or hung at the water supply pipe (figures 3.13 and 3.14). With reference to figure 3.13 water enters the controller from the supply pipe via a clear flexible hose (1). The end is plugged and drilled to retain large foreign materials in the water supply. Water enters the tank through a holed screw-on cap at the bottom of the controller (8). Five cm of small bore tubing is glued into the cap to ensure an even flow into the fish tank. The water level in the controller stabilises at an overflow port (7) cut in a pipe 25 mm in diameter (5). This pipe fits neatly over a similar 20 mm pipe (4) that leads to an overflow outlet (8). By sliding the larger pipe up or down over the smaller pipe, the water level can be set at any point over a range of about 20 cm.

Large changes in flow rate can be accomplished by changing the screw-on cap, and fine adjustment is carried out by altering the water level in the controller.

A preliminary trial was carried out to test the accuracy of a flow controller. Three caps were made with hole diameters of approximately 5 mm, 6 mm and 7 mm. These gave a total range of about 3.5 liters/minute to about 7.5 liters/minute - more than adequate for the application required. Timed collections of water enabled the calibration of each cap by regressing flow rate on water level in the controller. For the three caps, the correlation between flow rate and water level averaged 0.9987. The error involved here is sufficiently low for experimental purposes.

Increasing water temperature increased flow rate by about 0.1% per $1^{o}C$. This effect was considered to be negligible over the operational temperature range envisaged.

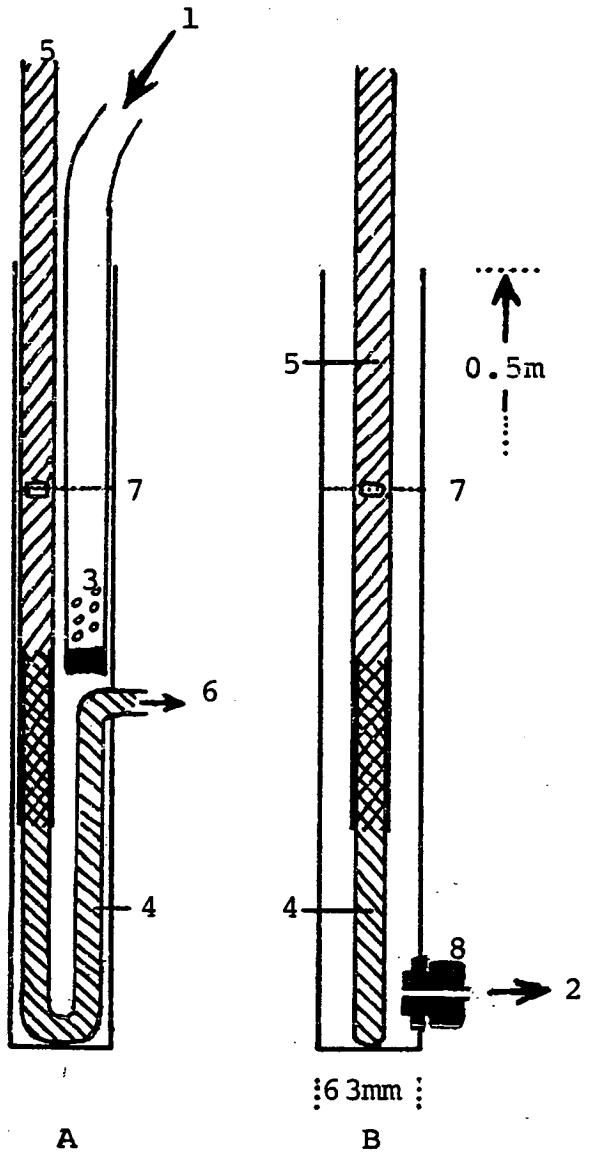

Figure 3.13 Water flow controller. One per tank.

Construction is based on 0.5 meter of 63 mm clear PVC tubing. A - rear view. B - side view. 1 - input from water supply. 2 - output to tank. 3 - filter. 4 - "U" tube. 5 - adjustment tube, this fits over the "U" tube. 6 - overflow to waste. 7 - water level in the controller. 8 - screw-on holed cap. Water level remains constant by overflow through an opening in the adjustment tube. Adjustment of flow rate is by replacement of holed cap (8) and/or raising or lowering adjustment tube (5).

Figure 3.14. A water flow controller mounted at the water supply pipe.

A further 40 caps were calibrated for use in the main experiment. In this case, timed collections were not necessary as standardised flow rates were available from the three caps described above. Each of the 40 caps was attached in turn to a "tester" controller which received water at standard flow rates from a second controller mounted above (figure 3.15). Stabilised water levels were recorded for various flow rates, and for each cap, a regression equation was calculated. These equations can be used to determine the water level required to give a desired flow rate.

A total of 36 controllers were constructed in November 1979. Material costs were about 50 N.kr. per unit. One controller was mounted at the water supply pipe adjacent to each of the 33 tanks in the experiment (figures 3.2 and 3.14). Three controllers were held in reserve.

The speed of flow through the holes in the screw-on caps proved sufficient to prevent any algal growth at operational temperatures. The inlet filters were cleaned about once every two months. No problems were encountered in the operation of these controllers.

At the beginning of each run during the 1979/80 season, the controllers were adjusted towards equalising the oxygen levels at the outlet of each tank in an attempt to equalise environments between tanks. Flow rates ranged from 4.24 liters/minute to 7.50 liters/minute.

With the introduction of a new system to prevent oxygen transfer across the water surface (section 3.2.3), the self cleaning of tanks was standardised during the 1980/81 season by setting all flow rates to 6.25 liters/minute.

Figure 3.15. Calibration of holed caps. The cap to be calibrated is screwed onto the "tester" controller below. At equilibrium, the water level in this controller is measured for each of a number of standardised flow rates from the controller mounted above.

Throughout the experiment DOC in the tanks was maintained at a level significantly above the minimum considered necessary for raising Rainbow trout (5 mgO_2/liter, various sources).

3.2.3. Covering of tanks.

At the beginning of the experiment all tanks were covered with heavy gauge polythene held down around the perimeter by a stretched loop of rubber (figures 3.2 and 3.11). Undersized holes were cut to accept the flow controller and automatic feeder giving airtight seals around these. Lowering the water level caused a suction downwards of the cover, indicating a reasonable degree of airtightness. About 250 liters of air was trapped under each cover.

The partial density of oxygen in air is 299 mg/liter - about 30 times that in the water under experimental conditions. For any given temperature, the ratio of oxygen concentration in the air to DOC is constant at equilibrium. Thus, exposure of fresh air under a cover to deoxygenated water in the tank will result in a proportional reduction of oxygen concentration in this air. Under experimental conditions this reduction is equivalent to a total transfer of about 15 grams of oxygen into the water. This is sufficient in quantity to maintain one tank of fish for about one day. A trial involving exposure of deoxygenated water to fresh air indicated that this transfer proceeds with a half life of several days.

In view of this, the opening of covers for adjusting feeders and cleaning tanks was considered too frequent during the 1979/80 season for the covers to have been of significant value.

This problem was largely overcome in the 1980/81 season by using floating plastic covers (figures 3.16 and 3.17).

Figure 3.16. Floating plastic covers as used in the 1980/81 season.

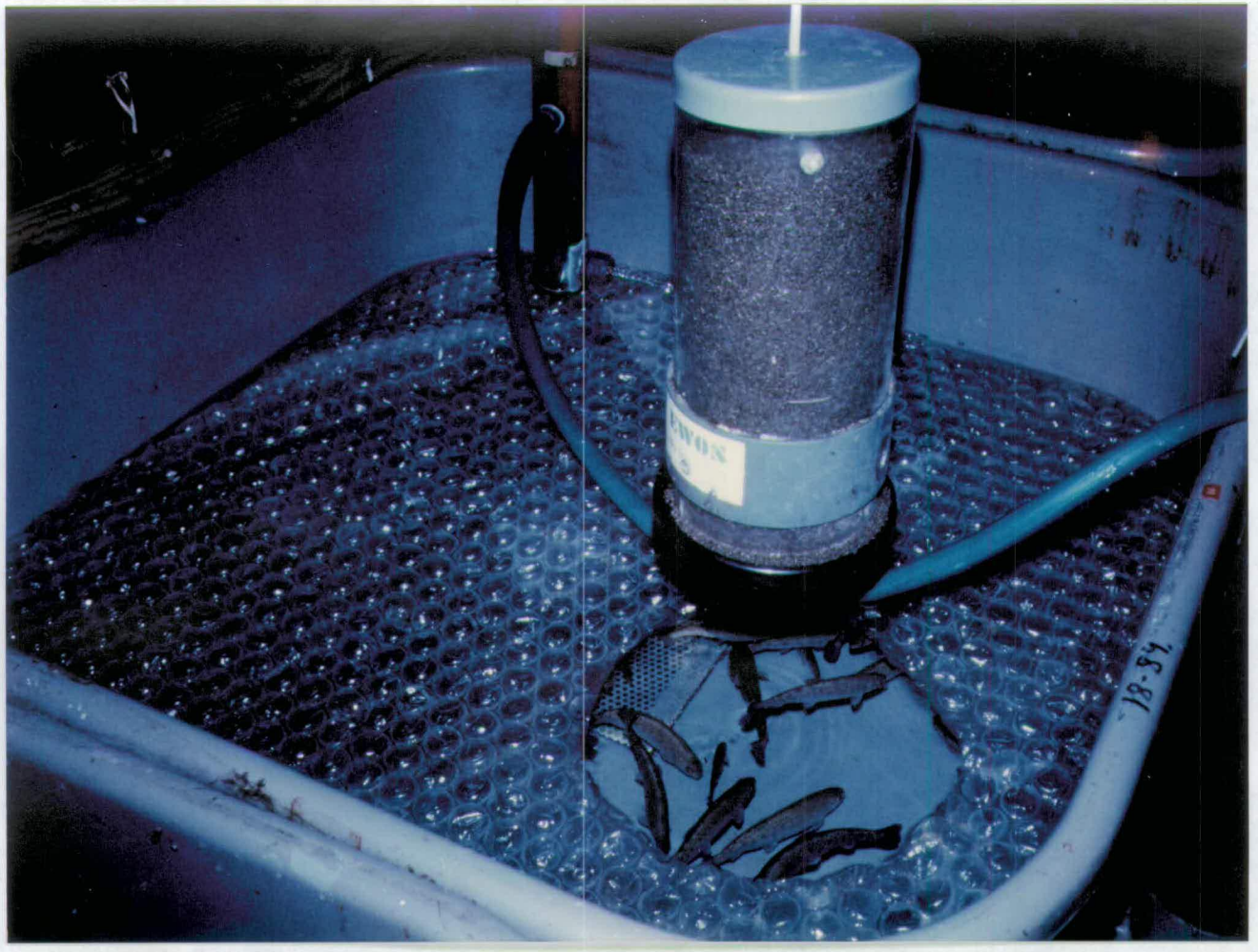

Figure 3.17. A floating plastic cover as used in the 1980/81 season.

Oxygen transfer across the water surface is restricted to those brief periods when the cover is lifted for cleaning or removing dead fish. A hole was cut below the automatic feeder for passage of food into the tank. Oxygen transfer here is minimal due to the small area of water exposed. Water from the flow controller falls directly onto the surface of the floating cover from where it passes into the main body of water at the feeder hole and the edges of the cover. As the inlet water is oxygen saturated, exposure of this water constitutes no significant oxygen transfer, and oxygen transfer at the feeder hole is minimised.

A major problem encountered with the floating covers was a reduction in water circulation within the tanks. This circulation is necessary to direct waste material to the central drain, and the reduction in this effect caused the tanks to require more frequent cleaning. Moreover, the build up of waste material in the tubes leading to the water sampler increased considerably. It is considered that tanks should be uncovered in any future work of this nature. A correction factor is then required to account for oxygen transfer across the water surface.

3.3. Processing of DOC recordings.

The data compiler (figure 3.3 f, and figure 3.6) was designed and constructed to concept specification by Mr. O. Haga of the Agricultural University of Norway.

A counter circuit in the compiler is stimulated once every full cycle or turn of the water sampler. The compiler maintains the following information in six memories:

1) A reference number (379) to identify the experiment.
2) The reading in the counter circuit.
3) The current DOC reading on a scale of 0 to 1000, which is linearly equivalent to 0 to 20 mg O_2/liter.
4) The state of a reference switch (on or off) located on the compiler. This acts to "time mark" selected lines of data.

5) Blank
6) Blank
} available for other applications.

The compiler is activated every one minute by photocell 18 (figure 3.5) to send the contents of each memory in turn to the data logger (figure 3.3 g). The quarter-inch magnetic tape mounted on the data logger was changed every six days. The data on these tapes was translated into a format suitable for the IBM 370 computer at the Agricultural University of Norway, and stored on 600 ft half-inch tapes.

Time marking of selected lines of data during experimental work aided the comparison of data files (about 8 500 lines of data per six day period) with written records of daily events in the running of the experiment.

For blockages of individual sample tubes, the corresponding datum or data were corrected by equating to the last valid oxygen reading in the data file. Where cleaning of sample tubes or other maintainance interfered with the proper recording of oxygen levels, one or two 35 minute cycles of data were erased.

Following correction of data, the mean DOC level was calculated for each of the 35 channels, and the mean rate of oxygen consumption of each group of fish was calculated as follows:

$$O_2 cons = \text{flow rate} \times \Delta DOC$$

(mg O_2/min = liters/min x O_2/liter)

where ΔDOC = (mean DOC of 2 inlet samples - mean DOC of tank outlet)

3.4. Feeding of the fish.

Tess trout pellets of size 4 and 4A (40% protein, 35% fat, 25% carbohydrate) were used throughout the experiment. Ewos automatic fish feeders were utilised, one per tank, as is normal practice at Sunndalsøra (figures 3.2 and 3.16).

This type of feeder consists of a hopper to hold up to 3 kg pelleted food, and a base plate from which a small quantity of food is dropped into the tank when an electric vibrator operates. All feeders in any one row are wired to a control unit which can be adjusted to operate the feeders for up to 4 seconds at intervals from 0.2 to 40 minutes.

During the first two runs, the base plates of the feeders were located under the tank covers (see section 3.2.3) where the humid atmosphere caused food delivery to be very erratic. This problem was so great during the second run that several groups of fish actually lost weight.

Following these problems, the fish were hand fed to excess (120 g/tank/day) during the third and fourth runs. Food was delivered 4 to 5 times daily through the holes vacated by the feeders. These holes were covered by removable caps at all other times.

During the 1980/81 season it was possible to use the automatic feeders with the introduction of a new system to cover the tanks (see section 3.2.3). In all runs an attempt was made to feed to excess without fouling the tanks with uneaten food.

The amount of food delivered to each tank in each run was recorded by volume.

3.5. Weighing of fish.

The total group weight of each full sib family (or replicate thereof) was taken at the start and end of each run as follows:

1) A Vega dial-type scale was zeroed with a trough of water and a large net placed on the weighing platform.
2) The net was placed over a bucket of water adjacent to the tank of fish to be weighed. All fish were removed from the tank by dip nets and placed in the net.
3) The net was taken from the bucket and raised and lowered until water run off was by individual drips (about 6 seconds).
4) The net was placed in the trough on the scale with the fish in the water.
5) If weighing at the start of a run, a sample of 5-10 fish was taken for chemical analysis.
6) A reading was taken and the fish were either put into their experimental tank (if weighing at the start of a run) or removed from the experiment after taking a second sample of 5-10 fish for chemical analysis.

Sampled fish were killed by immersion in a highly concentrated solution of anaesthetic (5% chlorabutanol), then stored in plastic bags and deep frozen within three hours.

Absolute growth of each group of fish was calculated as the increment in weight over the run plus the total weight of mortalities during that period. The rate of mortality during experimental runs averaged about one half of one percent.

3.6. Analyses of digestibility.

Analyses for digestibility of nitrogen and energy were carried out at the Institute of Poultry and Fur Animals of the Agricultural University of Norway, following the procedures of Austreng (1978). These procedures involve the collection of faeces from live fish. The quantity required for the estimation of energy digestibility (about 10 g) restricted this analysis to the small number of groups from which sufficient faecal material could be collected.

Although knowledge of energy digestibility (dg_e) can be used for the estimation of food consumption (see section 2), nitrogen digestibility (about 1 g faeces required) was considered to be of some value here, as it is known to be positively correlated with energy digestibility (Austreng, personal communication). Accordingly, faeces were collected from each group during the 1979/80 season and analysis for nitrogen digestibility was carried out for all groups in runs three and four.

Results of these analyses (section 4.1) were such that no digestibility analyses were carried out in the 1980/81 season.

3.7. Analyses of fish samples.

Samples of 5 to 10 fish (depending on fish size) were taken from each tank at the beginning of runs three and four before weighing and again at the end of these runs after weighing.

These samples were homogenized and analysed for percent (%) nitrogen, % dry matter, % ash and gross energy, at the Institute of Poultry and Fur Animals of the Agricultural University of Norway, following the procedure of Austreng et al. (1977).

% protein was calculated as 6.25 x % nitrogen (Austreng, 1978). Two estimates of % fat were calculated (Austreng, personal communication):

1) % fat = % dry matter - % protein - % ash

2) % fat =

$$\frac{\text{gross energy (kcal/100g fish)} - \%\ \text{protein} \times 5.7\ (\text{kcal/g prot.})}{9.4\ (\text{kcal/g fat})}$$

These equations assume that the carbohydrate content of whole fish is negligible.

4. ANALYSIS AND RESULTS

4.1. Traits involved in the experiment.

The traits and variables used in the analysis all relate to group observations, and are as follows:

1) Growth Growth is expressed as the mean daily increase in weight of the group as a percent of group weight at the start of the run. That is:

$$\text{Growth} = \frac{\text{Change in weight} \times 100}{\text{Weight at start} \times \text{duration of run (days)}} \quad \ldots\ldots \quad 4.1$$

This form is not quite the same as specific growth rate, but is more appropriate for calculation of food conversion efficiency, as food consumption is expressed on a similar basis.

2) Food cons. Food consumption is expressed as mean daily food consumption as a percent of group weight at the start of the run. Equation 2.3 was used as a basis in this calculation, giving:

$$\text{Food cons.} = \frac{100 \cdot k_1 \cdot O_2\text{cons.} + E_g}{ME} \quad \ldots\ldots \quad 4.2$$

- where k_1 = 3.31 calories per mg oxygen (section 2),
  ME = 3388 calories per gram food (Austreng, personal communication) and
  E_g = 2086 (cal/gm fish) x growth (as defined in equation 4.1)

The constant 2086 cal/gm fish was derived from the results of analyses of fish carcasses as described in section 3.7. Use of a constant here involves the assumption that the relationship between tissue energy gain (or loss) and

growth (positive or negative) is the same for all groups.

The use of nitrogen digestibility to help calculate food consumption (equation 2.2) was not carried out. This decision was taken following a preliminary analysis based on digestibility data from runs 3 and 4, which showed:

i) The coefficient of variation of nitrogen digestibility is very low (2.7%), indicating a low contribution to variation in true food consumption.

ii) The correlation between energy digestibility (the trait of interest) and nitrogen digestibility (the trait to be tested for every group) was 62±16%.

iii) There was some indication that nitrogen digestibility is lowly heritable - the heritability of family means being estimated at -7±24%.

3) GFCE Gross food conversion efficiency is expressed as growth divided by food consumed.

4) NFCE Net food conversion efficiency is expressed as

$$\frac{\text{Growth}}{\text{Food cons.} - \text{maintainance ration}}$$

The maintainance ration was estimated at 0.2499 gm/day/100 gm of fish (section 4.2). An obvious assumption here is that the efficiency of maintainance itself is the same for each group. The validity of this assumption is questioned in section 5.

5) O_2cons. Oxygen consumption is expressed as mg O_2 consumed per day per gram weight of group at the start of the run.

6) % fat Percent fat at the start of the run is expressed as the average of the results of the two derivations described in section 3.7. The correlation between the two methods was 62±8%.

7) Δ% fat Change in fat percent over the run was calculated on a similar basis as 6) above.

8) N digest Nitrogen digestibility in percent was calculated following analysis as described in section 3.6.

9) Mean Wt. The mean weight of fish in the group at the start of the run.

10) Age. The age of the group in days from hatching till the start of the run.

11) Input The mean daily delivery of food into the tank (g/day).

4.2. Phenotypic analyses.

4.2.1. The relationship between growth and food consumption.

Figure 4.1 illustrates the close relationship between growth and food consumption. Those growth observations which are low and negative are due to problems encountered with the automatic feeders, especially during runs 1 and 2. This information, however, facilitates the estimation of maintainance ration and weight loss on starvation. The linear regression of growth on food consumption is:

$$\text{Growth} = -0.36 + 1.45\ (\text{Food cons.})$$

A quadratic regression of growth on food consumption and its square resulted in a better fitting curve ($P<1\%$) with a marginal decrease in error variance (2.6%):

$$\text{Growth} = -0.43 + 1.61(\text{Food cons.}) - 0.074(\text{Food cons.})^2$$

S T A T I S T I C A L A N A L Y S I S S Y S T E M

PLOT OF GROWTH ON FOOD CONS. LEGEND: A = 1 OBS, B = 2 OBS, ETC.

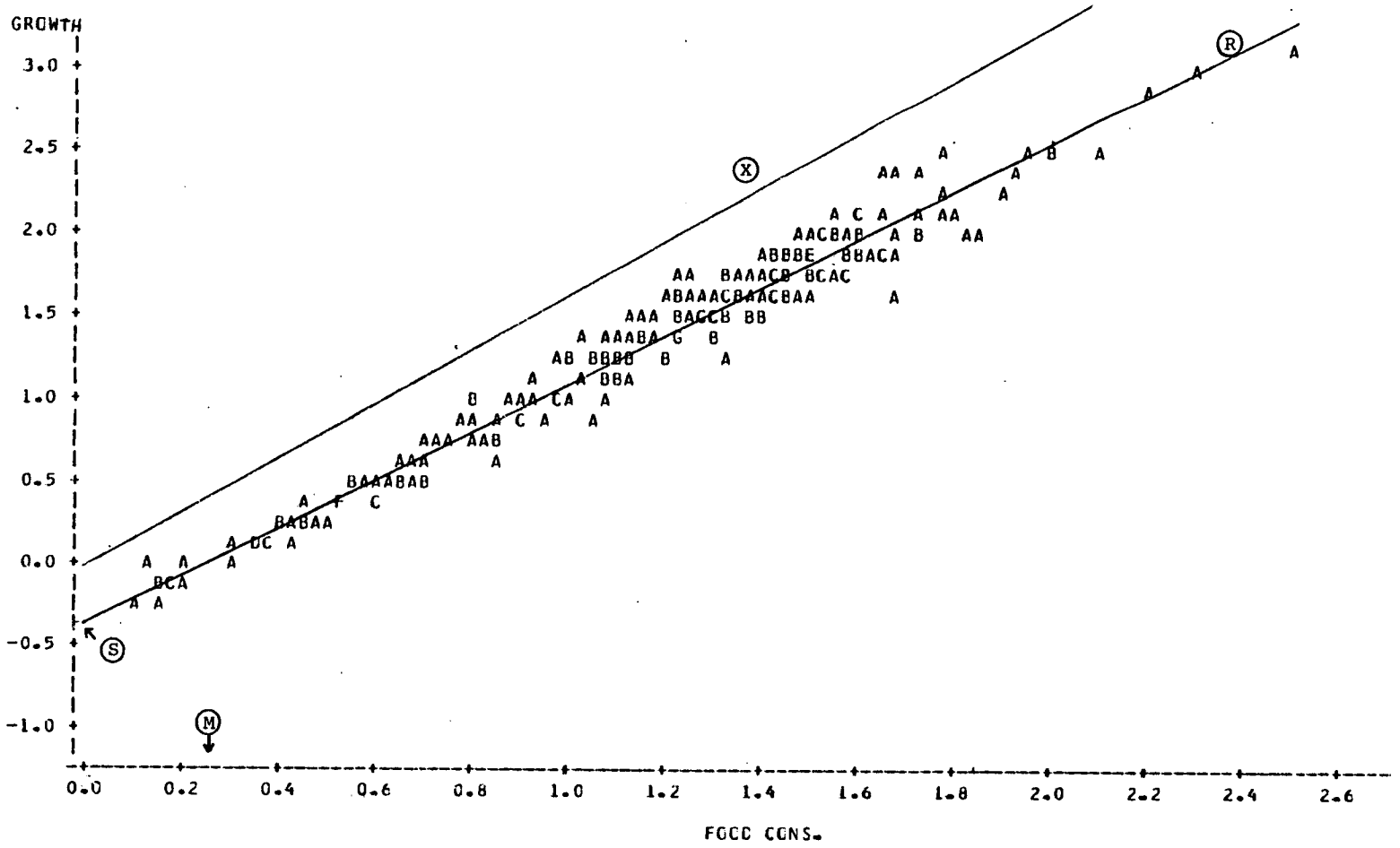

Figure 4.1. (opposite). The phenotypic relationship between growth and food consumption. Units for both traits are percent of group starting weight per day. R is the linear regression of Growth on Food cons.:

$$\text{Growth} = -0.36 + 1.45 \times \text{Food cons.}$$

M is the maintainance ration (0.25 percent) and S is starvation loss (0.36 percent). Regression X illustrates the contribution of growth to the estimate of food consumption (p_g (Food cons.)):

$$p_g(\text{Food cons.}) = \frac{2086}{3388} \times \text{Growth}$$

The derivation of this is apparent from inspection of equation 4.1. The contribution of total metabolic rate (i.e. oxygen consumption) to the estimate of food consumption (p_m (Food cons.)) is simply derived from regressions R and X:

$$p_m(\text{Food cons.}) = 0.25 + 0.073 \times \text{Growth}$$

S T A T I S T I C A L A N A L Y S I S S Y S T E M

PLOT OF GROWTH ON FOOD CONS. DATA FROM 1980/81 SEASON ONLY.

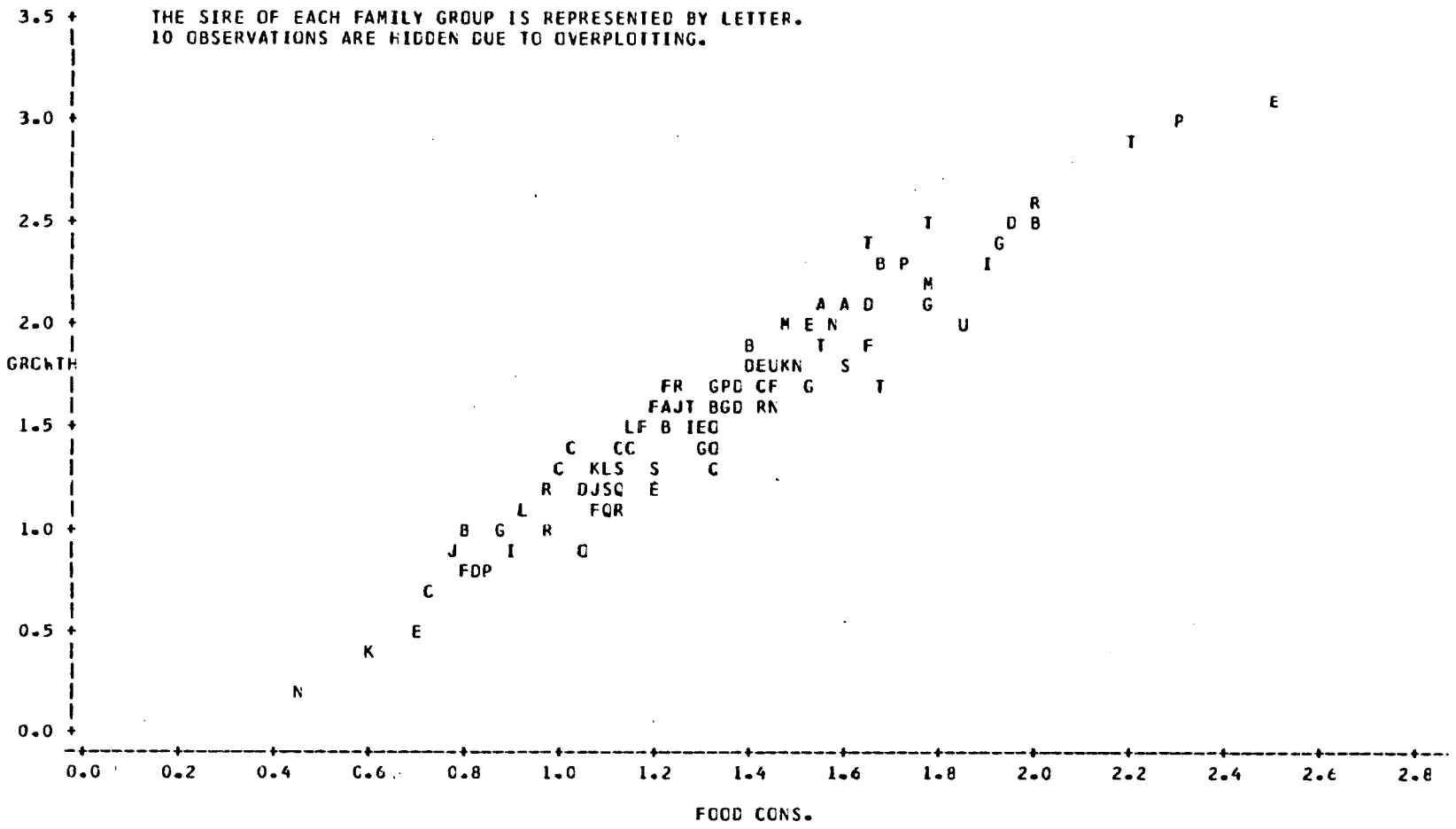

Figure 4.1b. (opposite). The phenotypic relationship between growth and food consumption. As for figure 4.1. except that each sire is represented by a different letter and data from the 1980/81 season alone are used.

However, this curve is a poor representative of those observations close to zero growth. The relationship seems to be linear up to about 1.5 percent Food cons., and curvilinear therafter, indicating the possible involvement of a threshold effect.

From the linear regression, maintainance ration is 0.25 percent of starting weight per day, and starvation loss is 0.36 percent of starting weight per day. Figure 4.1 shows that the contribution of metabolic rate to the estimate of food consumption ranges from 0.25 at zero growth to 0.47 at 3 percent growth.

It should be noted that there is an automatic correlation of errors between growth and food consumption due to any errors in weighing of fish. The effect of this can be described when the repeatability of growth measurement (R) is known. The following values relate to the linear regression under consideration:

V_g = variance of growth measurements = 0.491

V_{fc} = variance of calculated food consumption = 0.226

$Cov(g,fc)$ = covariance of these = 0.328

$b_{g,fc}$ = regression of measured growth on calculated food consumption.

$$= \frac{Cov(g,fc)}{V_{fc}} = 1.451$$

$r_{g,fc}$ = correlation of measured growth and calculated food consumption.

$$= \frac{Cov(g,fc)}{\sqrt{V_g \cdot V_{fc}}} = 0.985$$

Knowing the repeatability of growth, R, the following can be calculated:

V_e = variance in growth measurements due to errors in weighing.

$= (1-R) \cdot V_g$

V_{tg} = variance of true growth = $R \cdot V_g$

V_{tfc} = variance in true food consumption (i.e. food consumption calculated without error in growth measurement).

$= V_{fc} - K^2 V_e$

- where K is the contribution of the growth measurement to the estimate of food consumption. From inspection of equation 4.2, it can be seen that this is 2086/3388 = 0.616 grams food per gram fish.

Cov(tg,tfc) = the covariance of true growth and true food consumption.

$= Cov(g,fc) - K\ V_e$

Knowing Cov(tg,tfc), V_{tg}, and V_{tfc}, the values of the true regression and the true correlation (i.e. those values expected when growth is measured without error) can be calculated in the normal manner. Table 4.1 presents these for various values of the repeatability of growth measurement, R.

The repeatability of growth measurements was not tested because of the stress which would result from repeated weighings. However, a consideration of the observed variance in growth and all possible sources of error variance indicates that R is at least 95%. From table 4.1 it can be seen that this corresponds to a very minor effect on both the regression of growth on food consumption and the correlation between these traits.

Table 4.1. Values of the "true regression" of growth on food consumption and the "true correlation" between these for various values of the repeatability of growth measurement, R. See text for details.

R(%)	True regression	True correlation
100	1.451	0.985
95	1.444	0.985
90	1.436	0.984
80	1.417	0.983
50	1.330	0.980

For fast growing fish the gross food conversion efficiency was high, for example 1.27 at 2.5 percent growth, corresponding to 0.78 calories fish per metabolisable calorie of food.

As the present technique for estimating food consumption involves no food wastage, it might be expected that these figures should be equal to or higher than the most favourable figures gained elsewhere. This expectation is supported by the results of other workers presented in table 4.2.

Table 4.2. Gross food conversion efficiency in Rainbow trout. A: calories in fish/metabolisable calories in food. B: weight of fish/weight of food.

Approximate age or weight	Gross food conversion efficiency		Reference
	A	B	
Not given	-	0.85-1.18	Pieper and Pfeffer (1980)
1 year	-	0.44-1.00	Edwards et al. (1977)
1 year	0.13-0.64	-	Austreng et al. (1977)
70 g	-	0.52-0.62	Huisman (1976)
10 months	0.78	1.27	present results

4.2.2. The relationship between food consumed and input of food.

Figure 4.2 illustrates the relationship between food consumption and input of food expressed here in the same units (percent of starting weight per day). The high variation in food input is largely due to poor function of automatic feeders under plastic covers in runs 1 and 2 (section 3.2.3).

Three points to the upper left of the line of equality relate to groups which apparently consumed more food than they were offered. The error here is likely to be in measurement of food input which was carried out on the basis of volume delivered into the automatic feeders.

Under the hypothesis that there is a limit to appetite, the data were fitted to a segmented regression model in which food consumption increases curvilinearly with food input, but is unaffected by food input after the apex is reached (S.A.S. 1979: procedure "NLIN"). The regression equation is:

S T A T I S T I C A L A N A L Y S I S S Y S T E M

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

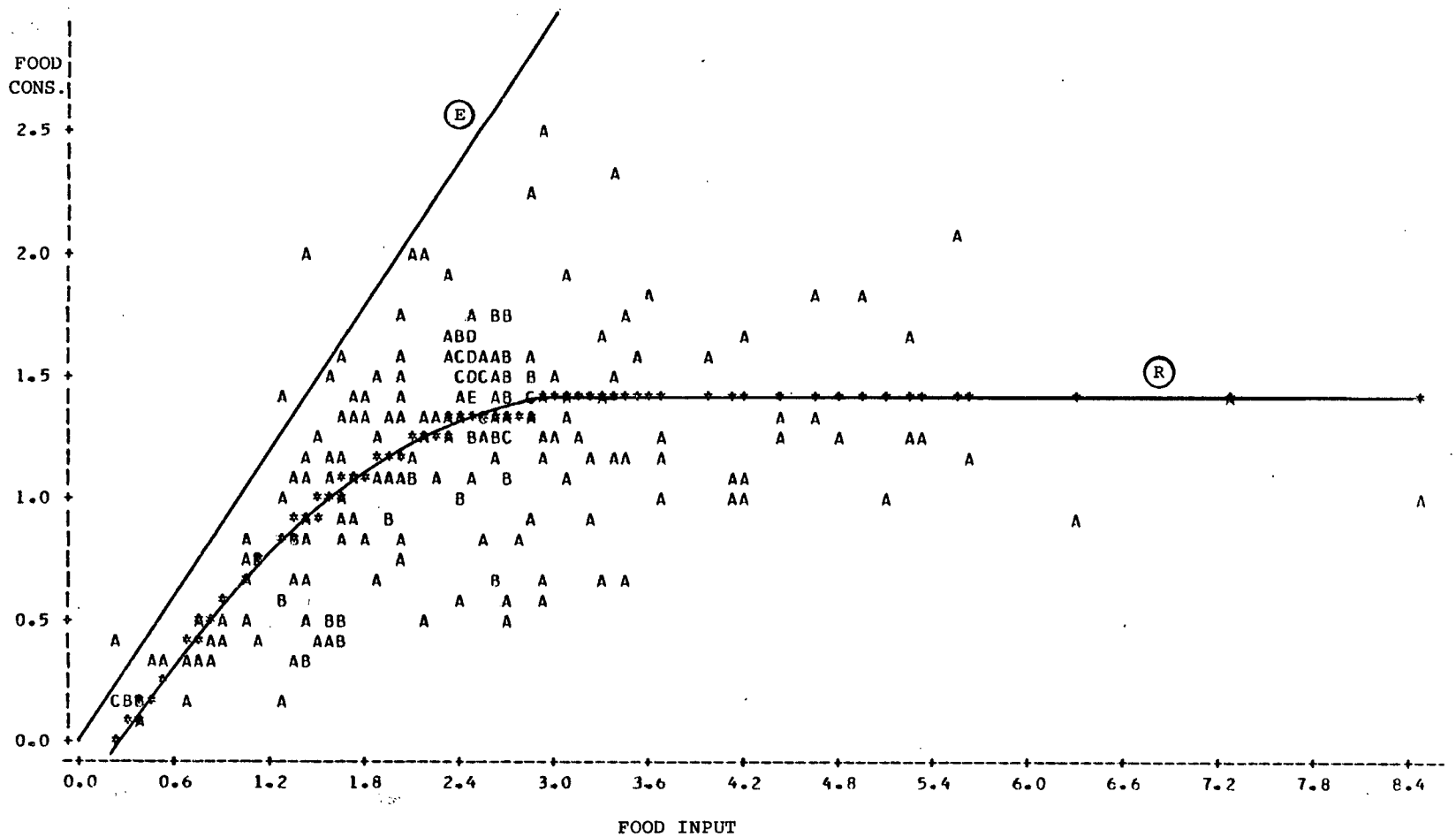

Figure 4.2 (opposite). The relationship between food consumption and input of food. Units are percent of group starting weight per day. E is the regression of equality (Food cons. = food input), which relates to groups which consume all the food they are offered. Points to the upper left of this line are presumed to involve errors in measurement of food input (see text). R is a segmented regression on the following model:

$$\text{Food cons.} = a + b.(\text{Input}) + c.(\text{Input})^2$$

with no effect of Input on Food cons. after the apex (see text), which is at

$$\text{Input} = \frac{-b}{2c} \qquad \text{(S.A.S. 1979)}$$

The least squares solution is given in the text.

$$\text{Food cons.} = -0.24 + 1.05(\text{Input}) - 0.17\ (\text{Input})^2$$

- and the apex is at 3.08 percent of group starting weight per day.

As might be expected, food wastage increases with increasing input of food. There is a weak indication that appetite is depressed at very high levels of food input.

4.2.3. Means and Correlations

Data from runs 1 and 2 are ommitted from this section because the low and negative growth figures involved are not normal (see section 3.2.3.). Data from one group in run 6 is also ommitted due to faulty operation of the automatic feeder in question. The mean daily input of food was only 14.4 grams (the mean for all other groups was 126.4) and this group lost weight over the run.

Table 4.3. presents the means and standard deviations of all traits described in section 4.1. The high variation in mean weight (range 17.0 g to 166.9 g) is due largely to differences in age (the correlation between these traits is 0.73), but is also a reflection of the high variation in weight for age found in most fish species.

The high variation in daily input of food (range 43 g/day to 334 g/day) reflects the difficulty in regulation of automatic feeders on a large scale. It is considered that this factor alone is responsible for much variation in growth traits, and that response to selection can be improved by adoption of a more suitable feeding system.

Table 4.4 presents correlations among the variables described in section 4.1. Several comments can be made about these results (with reference to table 4.4).

Table 4.3. Means and standard deviations of the traits involved in the experiment. See section 4.1 for description of traits and units used.

Trait	Mean	Standard deviation
Growth	1.626	0.463
Food cons.	1.361	0.316
GFCE	1.179	0.132
NFCE	1.465	0.126
O_2 cons.	3.681	0.911
% fat	9.715	0.938
Δ% fat	0.022	0.049
% protein	17.19	0.835
N digest	88.3	2.380
Mean weight	56.95	33.56
Age	261.5	41.61
Input	126.4	48.2

Table 4.4. Phenotypic correlations among variables 1-11, section 4.1 (above diagonal) and their significance (probability of obtained result under H : $r_p = 0$), (below diagonal). Correlations involving % fat, Δ% fat, or N digest are based on between 55 and 64 observations, those involving input are based on 98 observations and all others are based on 164 observations. a-o relate to comments in the text. Superscripts: potential source of positive (+) or negative (-) autocorrelation.

%	Grow	Food cons.	GFCE	NFCE	O_2 cons.	% fat	Δ% fat	N-digest	Mean wt.	Age	Input
Grow		96^{+a}	72^{+}	21^{+}	22^{b}	-23^{c}	27^{e}	33^{h}	-10^{-}	10^{j}	28^{o}
Food cons.	<1		53^{-}	-5^{-}	48^{+}	-27	36	33	-8^{-}	17	19
GFCE	<1	<1		79^{+}	-41^{-}	-15	11	32	-12	-6^{k}	47
NFCE	<1	55	<1		-85^{-}	5	-20	8	-10	-23	42
O_2 cons.	<1	<1	<1	<1		-20^{d}	42^{f}	11	5	28^{l}	-24^{p}
% fat	7	3	23	70	11		-67^{-g}	-30^{i}	15	7^{m}	-
Δ% fat	4	<1	40	14	<1	<1		32	-20	-19	-
N-digest	<1	<1	1	51	40	2	2		-22	-4^{n}	-
Mean wt.	20	33	11	19	52	24	14	8		73	-18
Age	20	3	42	<1	<1	58	15	73	<1		-34
Input	<1	7	<1	<1	2	-	-	-	8	<1	

a) Fish which consume more food grow faster but are not better net converters of food.

b) Fish which grow faster consume more oxygen.

c) Fat fish consume less food and grow more slowly, with no difference in net conversion efficiency.

d) Fat fish consume less oxygen, possibly due to lower activity.

e) Fish which consume much food deposit more fat. Fish which deposit more fat have a lower net conversion efficiency.

f) Fish which deposit more fat consume more oxygen, possibly due to the high energy cost of fat deposition.

g) Fat fish tend to deposit less fat, indicating the operation of a regulatory mechanism. The correlation between % fat at start and % fat at end of run (not shown in table 4.4) was 26±12%.

h) Fish which have a high nitrogen digestibility consume more food and may be better net converters of food. Correlations relating to this and the following comment are high in view of the low variance in nitrogen digestibility.

i) Fat fish which deposit less fat have a lower nitrogen digestibility.

j) Older fish eat and grow more, this effect seems to be independent of weight.

k) Older fish are poorer net converters of food, and, despite higher food consumption and growth, they are also poorer gross converters of food.

l) Older fish consume more oxygen, this effect seems to be independent of weight.

m) There is little indication that larger and older fish are fatter.

n) Smaller fish have higher nitrogen digestibilities, this effect seems to be independent of age.

o) Positive correlations between food input and growth traits are due to poor operation of the feeding system (low growth and conversion due to interuptions in feed supply) and efforts made to feed to excess (higher supply to high consuming groups).

p) Stress due to erratic food supply may contribute to the negative correlation between food input and oxygen consumption. This correlation supports the finding that the food itself does not consume oxygen (see figure 3.12).

It should be noted that these comments are open to personal interpretation with respect to both direction of cause-effect and significance. Wording is definitive for ease of reading.

Not shown in table 4.4 are the correlations between fat and protein percentages. These were -30±11% at the start of the run, -50±10% at the end of the run and -63±8% for change in percentages over the run.

4.3. Genetic analyses

4.3.1. Estimation of genetic parameters.

As all measurements in the experiment were taken on a group basis, variances within full sib families cannot be estimated and all genetic parameters must relate to family means.

A full analysis of the data would involve a nested model, dams within sires and replicates within dams. However, this type of model applied to the present data set leaves few error degrees of freedom for estimating genetic parameters from the sire components of variance and covariance. Accordingly, the effect of dam is ignored, and all models utilized are based on a one-way analysis of variance, group (full sib families and replicates) within sire.

In estimating family mean heritabilities, it is necessary to estimate the additive genetic variance between families from the sire component of variance. This component can be expressed in three parts:

$$\sigma_s^2 = 1/4V_a \cdot (1-r_s) + 1/4V_a \cdot P_r + 1/4V_d \cdot P_r \quad \ldots\ldots\ldots 4.3$$

(part I) (part II) (part III)

Part I is due to the average effects of the sires' genes. $(1-r_s)$ is a factor to correct for relationships between sires which result from intense selection on family index. r_s is the mean coefficient of relationship between sires.

Part II is the dam component of additive genetic covariance between groups within sire. P_r is the mean proportion of relationships within sire which are relationships between replicates. In a balanced design of D dams per sire and R replicates per dam,

$$P_r = \frac{R - 1}{DR - 1}$$

This formula is used to give approximations to P_r, using mean values of D and R relating to the data sets involved.

Part III is the dominance genetic covariance between groups within sire.

Note that parts II and III both equal zero in the absence of replication ($P_r = 0$).

The heritability of full sib family means in a population with no replication can be estimated as follows:

$$h^2_{fm} = \frac{V_a(fm)}{V_p(fm)} = \frac{2\sigma^2_s/(1-r_s+P_r)}{\sigma^2_s + \sigma^2_w} \quad \ldots\ldots\ldots\ldots \quad 4.4$$

- where σ^2_w is the component of variance within sire groups. This estimate is subject to two sources of bias:

i) a positive bias which can be calculated directly from equations 4.3 and 4.4. ...

$$\frac{\frac{1}{2} V_d \, p_r/(1-r_s+p_r)}{V_p(fm)}$$

Under the experimental designs involved, this bias is approximately equal to

$$\frac{V_d/20}{V_p(fm)}$$

ii) a negative bias due to reduction in genetic variance between sires caused by selection (Robertson, 1977). The magnitude of this bias is low where individual heritability is low. Estimates of individual heritability of weight in young Rainbow trout are generally low (see section 5). In view of this, it seems likely that the heritability of growth over a period of 3-4 weeks is also low. This indicates that selection bias is not of major importance for these traits.

The phenotypic correlation between full sib family means for traits 1 and 2 is:

$$r_p(fm)_{1,2} = \frac{Cov_p(fm)_{1,2}}{\sqrt{V_p(fm)_1 \cdot V_p(fm)_2}}$$

$$= \frac{Cov_s(1,2) + Cov_w(1,2)}{\sqrt{(\sigma^2_{s_1}+\sigma^2_{w_1})(\sigma^2_{s_2}+\sigma^2_{w_2})}} \quad .... \quad 4.5$$

- where $Cov_s(1,2)$ and $Cov_w(1,2)$ are the components of covariance of traits 1 and 2 between and within sires.

The additive genetic correlation between full sib family means for traits 1 and 2 is:

$$r_a(fm)_{1,2} = \frac{\frac{1}{2}Cov_a(1,2)}{\frac{1}{2}\sqrt{V_{a_1} \cdot V_{a_2}}} \doteq \frac{Cov_s(1,2)}{\sigma_{s_1} \cdot \sigma_{s_2}}$$

- as for values measured in individuals. Following an argument similar to that given above, it can be shown that this estimate of $r_a(fm)$ is biassed towards the dominance genetic correlation by approximately 25 % of the difference between these.

4.3.2. Genetic analysis of mean weights.

Mean weight within group at the start of the run is independent of experimental techniques. Moreover, this trait is used as an independent variable in the analyses of all other traits, and so mean weight is analysed separately here.

All 231 observations were included in the analysis, which was carried out within year due to absence of repeat mating. Analysis was by the least squares method according to the following model:

$$W_{ij} = S_i + bA_{ij} + e_{ij}$$

where

W_{ij} is the mean weight within the j^{th} group within the i^{th} sire as a deviation from the overall mean.

S_i is the effect of the i^{th} sire (considered as random).

A_{ij} is the age of j^{th} group within the i^{th} sire as a deviation from the mean age.

b is a partial regression coefficient of weight on age.

e_{ij} is the residual error effect on W_{ij}.

The analyses were carried out with the aid of the General Linear Models procedure of S.A.S. and effects were fitted simultaneously (Type IV analysis, S.A.S. 1979). An alternative model showed that a term in $(age)^2$ does not contribute significantly to the model sum of squares ($P = 12\%$ for 1979/80 data and $P = 78\%$ for 1980/81 data).

Table 4.5 presents the analyses of variance for the two seasons' data. The estimates of b were 0.76±0.06 g/day (1979/80) and 0.38±0.07 g/day (1980/81). This difference is associated with a higher range of ages in 1979/80

(215-341 days in 1979/80, 173-294 days in 1980/81) giving a curvilinear relationship in data pooled over years. However, there may be factors other than age contributing to the difference in b values between years (control of density in tanks, feed particle size etc.) and this curvilinearity may be an artifact.

Table 4.6 presents values of dams per sire (D), replicates per dam (R), proportion of replicate relationships within sire (p_r), mean coefficient of relationship between sires (r_s), family mean heritability derived from equation 4.4 (h^2_{fm}) and coefficient of variation for each year. Standard errors were calculated from the formula of Hill (1978).

Table 4.5. Analyses of variance for mean weight at start of run (Mean wt.).

Year	Source	d.f.	M.S.	F-value	Prob.>F(%)
	Sire	12	828	1.89	4.2
1979/80	Age	1	60 989	139.57	<1
	Error	118	437	-	-
	Sire	20	482	2.18	<1
1980/81	Age	1	5 991	27.05	<1
	Error	77	222	-	-

Table 4.6. Values of dams per sire (D), replicates per dam (R), proportion of replicate relationships within sire (Pr), mean coefficient of relationship among sires (r_s), family mean heritability (h^2_{fm}) and coefficient of variation (C.V.) relating to the least squares analyses of mean weight at start of run.

Year	D	R	p_r	r_s	h^2_{fm}	C.V.
1979/80	6.08	1.67	0.073	0.189	19±16	36
1980/81	3.43	1.38	0.101	0.152	43±23	41

4.3.3. Genetic analysis of experimental traits.

For reasons described previously in section 4.2.3, data from runs 1 and 2 and from one group in run 6 are omitted from this section.

Due to absence of repeat mating, this analysis was carried out within year. Heritabilities and genetic correlations were estimated for traits 1) - 8) (1979/80) and traits 1)-5) (1980/81) (see section 4.1) following analyses of variance by the least squares method.

1979/80 data were analysed by the following model:

$$Y_{ij} = S_i + b_1 W_{ij} + b_2 A_{ij} + e_{ij}$$

where

Y_{ij} is the dependent variable of the j^{th} group within the i^{th} sire as a deviation from the overall mean.

S_i is the effect of the i^{th} sire (considered as random).

W_{ij} is the mean weight of fish in the j^{th} group within the i^{th} sire at the start of the run as a deviation from overall mean weight.

A_{ij} is the age of the j^{th} group within the i^{th} sire as a deviation from mean age.

e_{ij} is the residual error effect.

b_1 and b_2 are partial regression coefficients of the dependent variable on mean weight and age respectively.

As 11 groups in the 1979/80 season have missing values for one or more of the traits % fat, Δ% fat and N digest, a separate analysis was carried out for all traits (1) - 8), section 4.1), ommitting data for the 11 groups concerned.

1980/81 data were analysed by the following model:

$$Y_{ij} = S_i + b_1 W_{ij} + b_2 A_{ij} + b_3 I_{ij} + b_4 I^2_{ij} + e_{ij}$$

where

I_{ij} is the mean daily food input to the j^{th} group within the i^{th} sire as a deviation from overall mean input.

b_3 is a partial regression coefficient of the dependent variable on food input and

b_4 is a partial regression coefficient of the dependent variable on the square of food input.

Food input is not involved in the 1979/80 model as this factor was standardised by hand feeding in this season (see section 3.4).

The analyses were carried out with the aid of the General Linear Models procedure of S.A.S. (1979) and effects were fitted simultaneously (Type IV analysis, S.A.S., 1979). Table 4.7 presents the analyses of variance for all experimental traits. Co-analysis of all dependent variables permitted calculation of the components of variance and covariance from the sums of squares and cross products matrices for sire and error.

Partial regression coefficients.

Table 4.8. presents the partial regression coefficients for mean weight (b_1), age (b_2), input (b_3) and input^2 (b_4). These are generally compatible with results presented in table 4.4 and the comments made in section 4.2.3. However, the effects of age on net food conversion efficiency and oxygen consumption appear to be opposite in the two years.

Presentation of genetic parameters.

Table 4.9 presents the values of dams per sire (D), replicates per dam (R), proportion of replicate relationships within sires (P_r) and the mean coefficient of relationship between sires (r_s) for each year. Tables 4.10 and 4.11 present family mean heritabilities (from equation 4.4),

Table 4.7. Analyses of variance of experimental traits.

Trait	Year	Source	d.f.	M.S.	F-value	Prob.>F(%)
Growth	1979/80	Sire	11	0.111	1.66	11
		Mean wt.	1	0.929	13.85	<1
		Age	1	0.251	3.74	6
		Error	52	0.067	-	-
	1980/81	Sire	20	0.276	1.58	8
		Mean wt.	1	0.412	2.37	13
		Age	1	3.073	17.66	<1
		Input	1	6.740	38.73	<1
		Input^2	1	5.403	31.05	<1
		Error	73	0.174	-	-
Food cons.	1979/80	Sire	11	0.055	1.76	9
		Mean wt.	1	0.393	12.53	<1
		Age	1	0.002	0.06	80
		Error	52	0.031	-	-
	1980/81	Sire	20	0.163	2.33	<1
		Mean wt.	1	0.386	5.52	2
		Age	1	2.623	37.52	<1
		Input	1	3.015	43.12	<1
		Input^2	1	2.43	34.70	<1
		Error	73	0.070	-	-
GFCE	1979/80	Sire	11	0.006	1.06	41
		Mean wt.	1	0.086	14.38	<1
		Age	1	0.158	26.44	<1
		Error	52	0.006	-	-
	1980/81	Sire	20	0.016	1.06	41
		Mean wt.	1	0.001	0.06	82
		Age	1	0.060	0.39	53
		Input	1	0.402	26.62	<1
		Input^2	1	0.306	20.28	<1
		Eror	73	0.015	-	-

Table 4.7. Cont.

Trait	Year	Source	d.f.	M.S.	F-value	Prob.>F(%)
NFCE	1979/80	Sire	11	0.005	1.10	38
		Mean wt.	1	0.010	2.43	13
		Age	1	0.147	35.68	<1
		Error	52	0.004	-	-
	1980/81	Sire	20	0.033	2.69	1
		Mean wt.	1	0.054	4.41	4
		Age	1	0.264	21.38	<1
		Input	1	0.039	3.12	8
		$Input^2$	1	0.023	1.85	18
		Error	73	0.012	-	-
O_2 cons.	1979/80	Sire	11	0.393	1.48	17
		Mean wt.	1	0.117	0.44	51
		Age	1	7.325	27.60	<1
		Error	52	0.265	-	-
	1980/81	Sire	20	1.877	3.62	<1
		Mean wt.	1	5.336	10.28	<1
		Age	1	30.593	58.96	<1
		Input	1	1.986	3.83	5
		$Input^2$	1	1.672	3.22	8
		Error	73	0.519	-	-
% fat	1979/80	Sire	11	1.668	2.08	5
		Mean wt.	1	0.498	0.62	44
		Age	1	0.113	0.14	71
		Error	41	0.803	-	-
Δ% fat	1979/80	Sire	11	0.003	1.20	32
		Mean wt.	1	0.001	0.52	48
		Age	1	0.001	0.23	64
		Error	41	0.002	-	-
N-digest	1979/80	Sire	11	5.280	0.88	56
		Mean wt.	1	14.140	2.36	13
		Age	1	2.410	0.40	53
		Error	41	5.984	-	-

Table 4.8. Estimates of partial regression coefficients from the least squares analyses. b_1 - mean weight, b_2 - age, b_3 - food input, b_4 - input^2. Estimates relating to fat traits and N digest were all non-significant. See section 4.1 for units. Significance of difference from zero: (.)P<10%, (..)P<5%, (...)P<1%.

		Growth	Food cons.	GFCE	NFCE	O_2cons.
1979/80	$b_1 \times 10^4$	-51...	-33...	-16...	-5.3	-18
	$b_2 \times 10^4$	43.	3.8	34...	33...	-231...
1980/81	$b_1 \times 10^4$	-49	-48..	2	18..	-177...
	$b_2 \times 10^4$	112...	103...	-5	-33...	353...
	$b_3 \times 10^3$	212...	142...	52	161.	115.
	$b_4 \times 10^4$	-53...	-35...	13...	-3	-29.

Table 4.9. Values of dams per sire (D), replicates per dam (R), proportion of replicate relationships within sire (p_r) and mean coefficient of relationship among sires (r_s) relating to the least squares analyses of experimental traits.
a) relates to the full data set for runs 3 and 4,
b) relates to the reduced data set after elimination of lines with missing values for one or more of % fat, Δ% fat and N digest.

Year	D	R	p_r	r_s
1979/80 a)	4.08	1.35	0.077	0.219
1979/80 b)	3.50	1.31	0.086	0.219
1980/81	3.43	1.36	0.098	0.152

Table 4.10 Family mean heritabilities (diagonal), genetic correlations (above diagonoal) phenotypic correlations (below diagonal), coefficients of variation (after fitting of covariables) and means from least squares analyses of data from runs 3 and 4 (1979/80). Percentage units. Estimates involving fat and digestibility traits were derived from analysis of a different data set (11 lines of data missing) *P<10%, **P<5%, ***P<1%, all C.V.values are significant.

	Growth	Food cons.	GFCE	NFCE	O_2 cons.	% fat	Δ% fat	N digest	CV	$\bar{x}$
Growth	27±28	99± 4***	101±28***	-31±140	66±72	-47±70	70±143	-	13.4±2.4	1.67
Food cons.	96± 1***	30±28	84±50	-54±116	78±49	-40±69	82±123	-	16.4±2.9	1.42
GFCE	79± 5***	64± 8***	3±21	-5 ±552	- 2±156	-	-	-	6.6±1.2	1.17
NFCE	28±13**	3±13	75± 6	5±22	-123± 55**	-	-	-	4.5±0.8	1.43
O_2 cons	25±13*	50±10***	-22±13*	-79 ± 5***	20±20	-	-	-	13.6±2.4	3.96
% fat	-23±15	-28±14**	-15±15	9 ± 16	-27± 14*	47±34*	-71± 42	-	10.3±2.0	9.71
Δ% fat	24±15	32±14**	15±15	-16 ± 15	39± 13***	-68± 8***	10±20	-	245±48	0.02
N digest	21±15	22±15	24±15	5 ± 16	10± 15	-28±14**	29± 14**	-7±24	2.7±0.5	87.90

Table 4.11. Family mean heritabilities (diagonal), genetic correlations (above diagonal), phenotypic correlations (below diagonal), coefficients of variation (after fitting of covariables) and means from the least squares analysis of 1980/81 data. Percentage units.

%	Growth	Food cons.	GFCE	NFCE	O_2cons.	C.V.	$\bar{X}$
Growth	25±21	99± 2***	-211±373	-95±48*	93±28***	27.9±4.1	1.59
Food cons.	96± 1***	50±24**	-203±192	-98±29***	97±16***	22.9±3.4	1.32
GFCE	62± 7***	40±10***	3±18	176±46***	-182±61***	10.4±1.5	1.18
NFCE	15±11	-13±12	81±4***	59±24**	-100±3 ***	8.8±1.3	1.49
O_2cons.	18±11	45±9***	-54±8***	-88±3***	80±24***	26.1±3.8	3.49

*P<10%,
**P< 5%,
***P< 1%, all C.V. values are significant.

Table 4.12. Estimates of family mean heritabilities (diagonal), genetic correlations (above diagonal), phenotypic correlations (below diagonal), coefficients of variation and means combined from results given in tables 4.10 and 4.11 for 1979/80 and 1980/81 data respectively. $\bar{X}$ values are simple means and all other estimates are error weighted means. All estimates differ significantly from zero (P<1%) except those marked + (P<5%), ‡ (P<2%) and ^{o} (not significant).

%	Growth	Food cons.	GFCE	NFCE	O_2 cons.	C.V.	$\bar{X}$
Growth	26±12‡	99±1	80±26	-79±36+	85±20	18.8±1.5	1.63
Food cons.	96±1	41±13	25±40	-89±23	93±12	19.5±1.6	1.37
GFCE	72±3	53±4	3±10^{o}	162±43	-131±44	8.3±0.7	1.18
NFCE	21±6	-5±6^{o}	79±2	31±11	-101±3	6.2±0.5	1.46
O_2 cons.	21±6	48±5	-42±5	-85±2	51±12	18.3±1.5	3.73

phenotypic correlations (from equation 4.5), genetic correlations (from equation 4.6) and coefficients of variation for each year. Table 4.12 presents estimates combined over years with weighting by the inverses of standard errors.

Standard errors of heritability estimates were calculated according to Hill (1978). Standard errors of genetic correlations were calculated according to Robertson (1959, page 473). This procedure requires the use of the calculated value of the genetic correlation as an estimator of the true value. As the error distribution is greatly reduced at true values of 1 and -1, caution must be exercised in interpreting standard errors of estimates close to these values. Genetic correlations are not given where negative estimates of heritability are involved, as these would be meaningless.

There are no significant differences between years in the estimates of heritabilities and correlations (P>5%), but such differences do exist for coefficients of variation. It seems likely that this is at least partly due to adoption of hand feeding in 1979/80. Although mean daily input of food is included in the model for the 1980/81 analysis, this measurement does not describe the regularity of food input.

It should be noted that parameters are estimated with simultaneous correction for the covariables in the model, and they should be considered relevent only to breeding programs involving such correction.

5. DISCUSSION

The similarities between phenotypic correlations from raw data (table 4.4) and phenotypic correlations from least squares analyses (table 4.10 for correlations involving % fat, Δ% fat or N digest; table 4.12 for all other correlations) show that the covariables in the models used have no large effects on these relationships.

The combined estimate of family mean heritability for mean weight (29±9%, C.V. = 38%) compares well with that found by Kincaid (1972) for 150 day weight (26±12%), and is compatible with the rather low individual weight heritabilities estimated from previous year classes at Sunndalsøra - 9±10% at 150 days and 29±20% at 280 days (Aulstad et al., 1972) and 6% at 140 days (Refstie, 1980). After linear absorbtion of age effects the phenotypic coefficient of variation between families remains high (combined estimate 38%). This is typical of young fish, and compares with Refstie's (1980) 52% coefficient of variation between individuals for weight at 140 days.

The family mean heritabilities for growth and food consumption are both moderate and quite significant (26±12% and 41±13% respectively). This might be taken as an indication that genetic variation in these traits follows the slope of growth regressed on food consumption (figure 4.1). If this were the case, GFCE would be expected to be similarily heritable, as variation in this trait is the same as the variation in the slopes from the origin (growth = 0, food cons. = 0) to each point in figure 4.1.

However, from table 4.12 it can be seen that this is not the case (h^2_{fm} = 3±10%). The situation is clarified by

inspection of the regression of sire effects for growth (SG) on sire effects for food consumption (SFC) (figure 4.3). As estimates of sire effects involve some environmental error, this can only be considered as an approximation to the true genetic regression, being biassed towards the phenotypic regression. Nevertheless, the slope and intercept of this regression differ ($P<10\%$) from those of the phenotypic regression calculated from the same data set.

$$SG = -0.08 + 1.25\ SFC$$

$$\text{Growth} = -0.29 + 1.41\ \text{Food cons.}$$

The reason for this reduction in slope is that growth is less heritable than food consumption - the slope would be zero if there were no variation in SG.

From figure 4.3 it can be seen that genetic variation in GFCE is low (the regression intercept is close to the origin), but genetic variation in NFCE is higher (this variation is equivalent to variation in the slopes from the coordinate (SG = 0, SFC = maintainance ration) to each point).

These considerations, plus the fact that phenotypic variance in GFCE is greater than that in NFCE, illustrate the basis for the low (GFCE) and high (NFCE) family mean heritabilities (3±10% and 31±11% respectively).

The fact that the correlations between growth and food consumption are close to unity (r_p = 96%, r_g = 99% and r_e = 96%) permits the use of a simple model to further illustrate the relationship between these traits.

For ease of illustration, it is assumed that $r_g = r_e = 1$. Figure 4.4 depicts the population range of breeding values and environmental deviations as the appropriate linear

S T A T I S T I C A L A N A L Y S I S S Y S T E M

PLOT OF SIRE EFFECT FOR GROWTH (SG) ON SIRE EFFECT FOR FOOD CONSUMPTION (SFC) LEGEND: A = 1 OBS, B = 2 OBS, ETC.

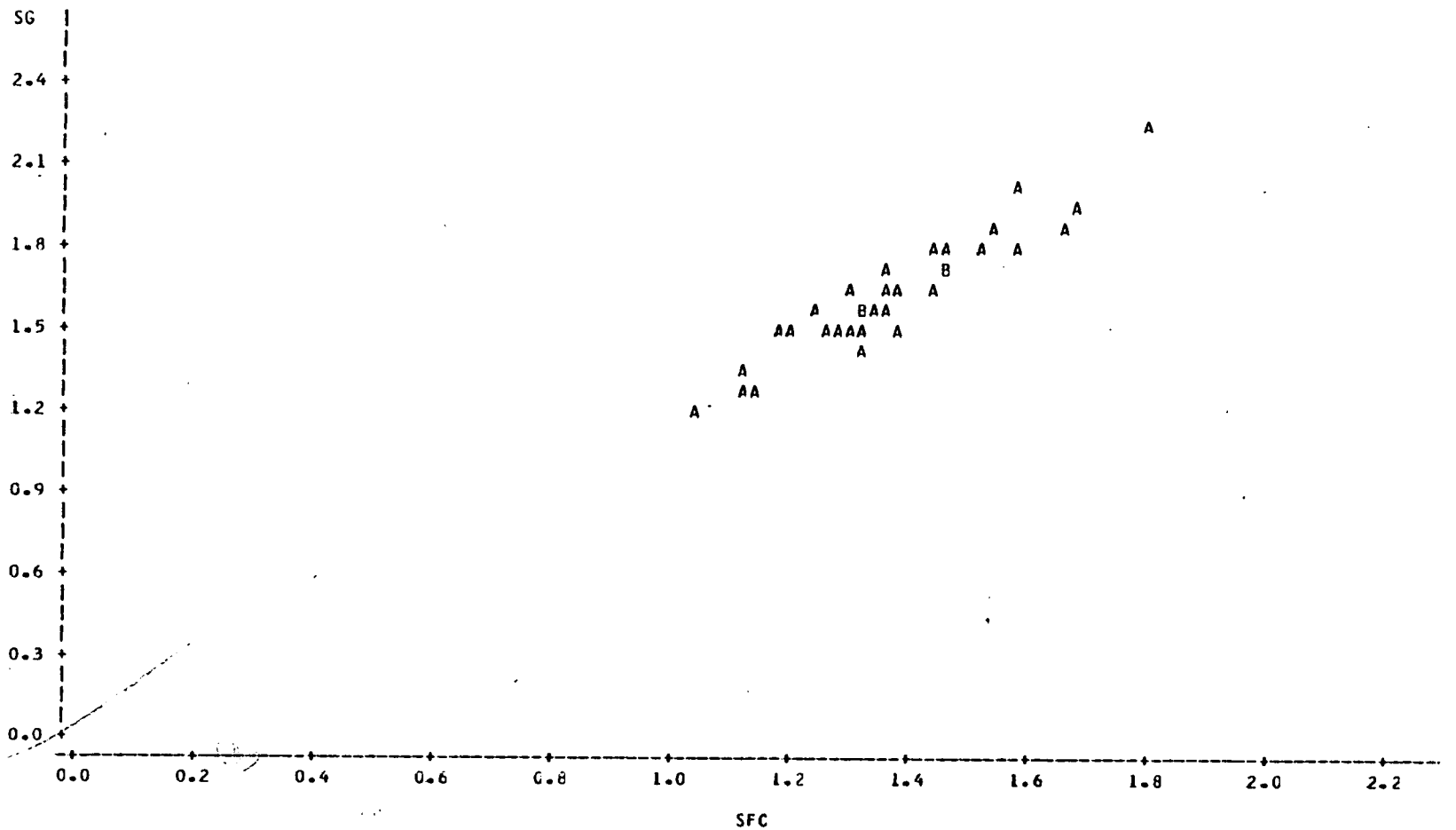

Figure 4.3 (opposite). The relationship between sire effects for growth (SG) and sire effects for food consumption (SFC). Means of both these variables are set to the population mean. Units are percent of group starting weight per day. The linear regression is:

$$SG = -0.08 + 1.25 \times SFC$$

As estimates of sire effects involve some environmental error, this can only be considered as an approximation to the true genetic regression which is biassed towards the phenotypic regression.

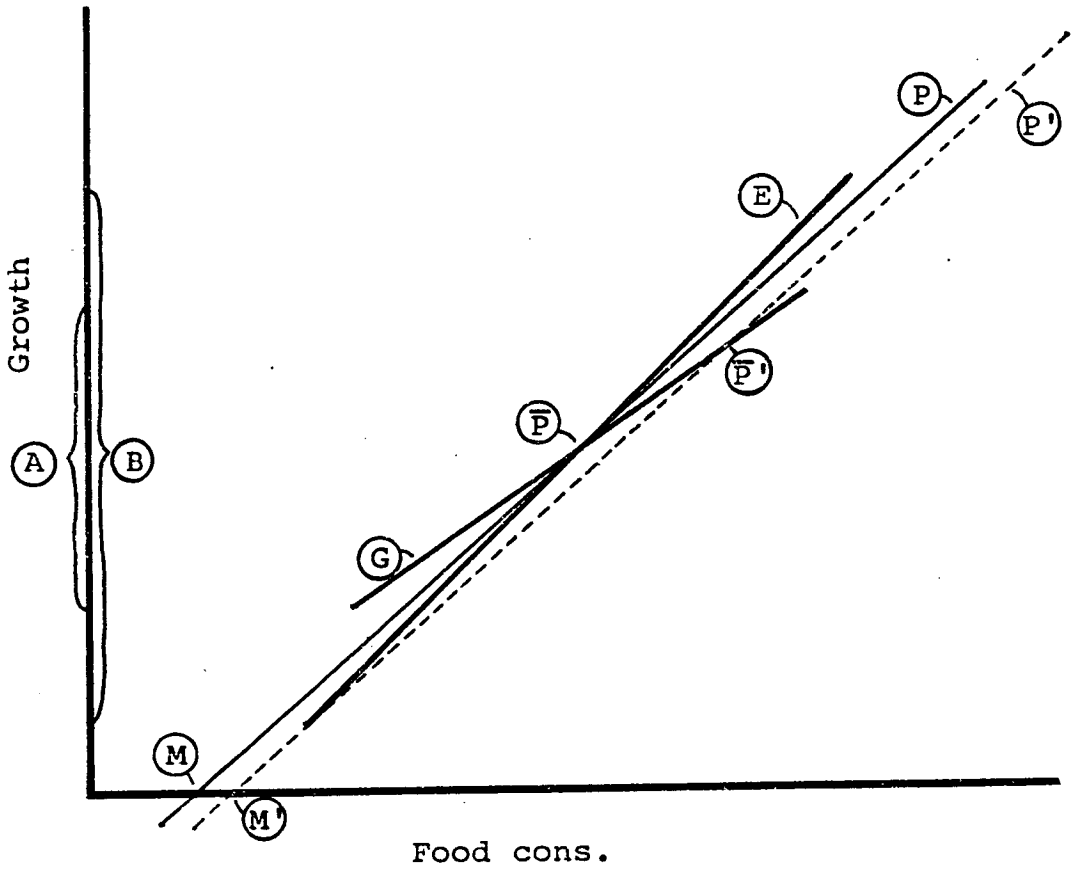

Figure 4.4. A simple model to illustrate the genetic relationship between growth and food consumption. r_g = r_e = 1 is assumed. G,E and P are the genotypic, environmental and phenotypic regressions of growth on food consumption, with all means equated to the population mean $\bar{P}$. M is maintainance ration. The lengths of lines G and E reflect the magnitudes of genotypic and environmental standard deviations in each dimension. For example, the ratio of the vertical lengths of G to E is:

$$A:B = SD_g(\text{Growth}) : SD_e(\text{Growth})$$

$$= h_{fm}(\text{Growth}) : \sqrt{1-h^2_{fm}(\text{Growth})}$$

With genetic progress, the population mean moves to $\bar{P}'$, the maintainance ration increases to M', and P' is the new phenotypic regression.

regressions of growth on food consumption (lines G and E respectively), the mean of each regression being set to the population mean. The relative lengths of the lines G and E reflect the genetic and environmental variations in growth and food consumption (h_{fm}: $\sqrt{1-h^2_{fm}}$ on the axis of each trait). When added as deviations from the population mean, points randomly chosen on lines G and E can be used to give the phenotypic regression (line P). Note that not all resulting points lie exactly on P, because G and E are not parallel. This illustrates that r_p must be less than unity when the heritabilities differ, unless both heritabilities are zero.

With genetic response to selection, the population mean moves along line G and the phenotypic regression changes to P'. An important prediction on this simple model is that the maintainance ration increases from M to M'. As line G passes close to the origin, there is expected to be little response in either gross or net food conversion efficiency.

In view of this, it is noted that the family mean heritability for net food conversion efficiency given in table 4.12 (h^2_{fm} = 31±11%) is misleading as it assumes a constant maintainance requirement for each group.

The family mean heritability of oxygen consumption is moderately high (51±12%, C.V. = 18.3%), but this is a trait of little direct commercial value, except possibly where water recirculation is utilized. However, its apparently high genetic correlation with growth precludes downward selection on oxygen consumption.

There is some indication that percent fat in the body (% fat) is moderately heritable (h^2_{fm} = 47±34%, C.V. = 10.3%). Refstie and Austreng (1981) found significant

differences in fat percent between 10 full sib families of young Rainbow trout (P<5%). Ayles (1979) reports additive and non-additive differences in lipid content of four Rainbow trout strains and their crosses. However, there is a weak indication that the genetic correlation between growth and fat deposition (Δ% fat) is positive (r_g = 70±143%, r_p = 24±15%) which is an unfavourable relationship. At present, wholesale prices for farmed Rainbow trout are not affected by fattiness of the fish, but this situation may change as the market develops. Strong selection on growth alone may result in the development of an unmarketable product.

Nitrogen digestibility was found to have little variation with no heritability (h^2_{fm} = -7±24%, $C.V._{fm}$ = 2.7%). However, Gjedrem (unpublished) has found a moderate heritability for this trait with similar variation (h^2_{fm} = 34±12%, $C.V._{fm}$ = 2.3%) in data from 15 full sib families of Rainbow trout. This heritability estimate may be biassed upwards as it is calculated from the dam component of variance. The two estimates do not differ significantly.

6. CONCLUSION

It is proposed that consideration of food consumption is of little or no value when selecting young Rainbow trout. This is of most relevence to production of portion sized fish in fresh water, as is widely practised in continental Europe and Britain. There is little information available about the correlation of growth traits during the freshwater stage and the sea water stage in the production of large (2-5 kg) fish, and the relevance of the present results to this type of production must remain in doubt.

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ACKNOWLEDGEMENTS

I would like to thank the following :

Professor Alan Robertson, my supervisor, for much support and advice under circumstances often made difficult by distance.

Professor Harald Skjervold, for introducing me to the concept of using oxygen consumption to help estimate food consumption and for continued interest in my experimental work.

Dr. Trygve Gjedrem, for use of experimental facilities at the Research Station for Salmonids, Sunndalsøra, and for many interesting discussions.

Mr. R. Markussen and staff of the Institute of Physics, Agricultural University of Norway, for help in construction of the water sampling machine.

Mr. Oddvar Haga of Instrumenttjenesten, Agricultural University of Norway, for constructing the data compiler.

Mr. Gerry Flynn and Mr. Svein Hjeldnes, for valuable technical assistance in setting up and maintaining the experimental work at Sunndalsøra.

Dr. Erland Austreng and staff of the Institute of Poultry and Fur Animals, Agricultural University of Norway, for analysis of fish and faeces samples.

Mrs. Conny Kinghorn, my wife, for much assistance in technical work and quality control.

Mrs. Marianne Lunde, for typing the thesis.

I would also like to thank the staff of the Institute of Animal Breeding and Genetics, Agricultural University of Norway, for the many kindnesses they have shown to me and my family during our stay in Norway.

LIST OF PAPERS SUBMITTED DURING THE PERIOD OF REGISTRATION

LIST OF PAPERS

*Kinghorn 1980, A model for the optimisation of genetic improvement by the introduction of novel breeds into a native population. Z. Tierzücht. Züchtbiol. (Journal of Animal Breeding and Genetics) 97 : 95-100

*Kinghorn 1980, The expression of 'recombination loss' in quantitative traits. Z. Tierzücht. Züchtbiol. 97 : 138-143

+Kinghorn 1980, The use of oxygen consumption as an indicator of energy assimilation in Rainbow trout. 31st meeting E.A.A.P. Munich, Sept. 1980. Paper G 5.16

Kinghorn 1981, Non additive components of merit in crossbred mice. 32nd meeting, E.A.A.P., Zagreb, Sept. 1981. Paper G 3.7

Kinghorn 1981, Genetic effects in crossbreeding. I. Models of merit. Z. Tierzücht. Züchtbiol. (In press)

+Kinghorn 1981, A water flow controller. The Progressive Fish Culturalist. (In press)

+Kinghorn 1981, A system for monitoring water quality at many sources. The Progressive Fish Culturalist. (In press)

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+Kinghorn 1981, Norwegian advances in fish breeding. Poultry Round Table. 24-25 Sept. Edinburgh.

Kinghorn 1981, Review of: Atlantic salmon - its future. Proc. II Int. Symp. on Atlantic salmon. Sept., 1978. Ed: A.E.Went. Fishing News Books, UK. Aquaculture 23 383-384.

Papers marked + are directly related to the subject of this thesis. Papers marked * are bound at the end of this thesis as an appendix.

Sonderdruck aus Zeitschrift für Tierzüchtung und Züchtungsbiologie
Bd. 97 (1980), H. 2, S. 138-143

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The expression of "Recombination Loss" in quantitative traits

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Ms. received 9. 1. 1980

In generating individuals whose genes are derived from more than one breed, we aim to exploit favourable dominance deviations. However, we run the risk of breaking down favourable epistatic relationships which have been established within the breeds. Epistasis here refers to all non-allelic gene interactions.

The relationship between the expression of such a breakdown (recombination loss) and the total genotype of an individual is the subject of discussion here. In parts, this phenomenon will be discussed in situations where no recombination has taken place. Accordingly, the term 'epistatic loss' will be used hereafter.

Consider two unlinked but interacting loci P and Q in an F_1 cross between breeds A and B. The genotype of this individual can be represented thus:

$$\frac{P_A}{P_B} \qquad \frac{Q_A}{Q_B}$$

Does this individual suffer a breakdown of favourable epistasis, and if so, what proportion is this of the mean epistatic loss (e) in the individuals:

$$\frac{P_A}{P_A} \quad \frac{Q_B}{Q_B} \qquad \text{and} \qquad \frac{P_B}{P_B} \quad \frac{Q_A}{Q_A}$$

– where no 'within breed' epistatic interaction occurs?

The answer to this depends on the nature of the interaction between loci P and Q. Two hypotheses can illustrate this:

Hypothesis X: Genes P and Q both code for a different component of a dimorphic enzyme, with association of components at random. If there is no difference 'between breeds' in quantities of the two components manufactured, half of these enzyme molecules will be hybrid with respect to breed of origin. Thus the epistatic loss in the F_1 cross will be 0.5e.

Hypothesis Y: Genes P and Q code for independently operating enzymes which are involved in the same biochemical pathway. Here there should be no epistatic loss in the F_1 cross (although complementation could result in an epistatic gain).

If hypothesis X were universal, epistatic loss would be proportional to the probability that two non-allelic genes randomly chosen in the diploid individual are of different breed origin.

If hypothesis Y were universal, the epistatic loss would be proportional to the probability that both genes of a randomly chosen locus are of different breed origin to that of a non-allelic randomly chosen gene. This involves an assumption which is best illustrated by stating that the following two individuals should have the same benefit from epistatic interaction between genes of breed A:

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Z. Tierzüchtg. Züchtgsbiol. 97 (1980) 138–143

ISSN 0044–3581/ASTM-Coden: ZTZBAS

etc.) and a knowledge of the population structure. The "basic values" of the nc breeds, (X_i; i = 2, . . ., n) are taken from animals introduced in year 2. Respons selection in the nucleus units subsequent to year 2 is considered over and above basic value. If, for now, we ignore "non-additive" effects, the following apply a introductions in year 2: –

Total frequency of introduced animals after corrections $= \sum_{i=2}^{n} Z_{i,2}$

Mean value of these animals $= \dfrac{\sum_{i=2}^{n} Z_{i,2} X_i}{\sum_{i=2}^{n} Z_{i,2}}$

Total frequency of non-introduced animals $= 1 - \sum_{i=2}^{n} Z_{i,2}$

Mean value of these animals $= X_1$

$$\bar{G}_2 = \sum \text{ (frequency} \times \text{value)} = (1 - \sum_{i=2}^{n} Z_{i,2})X_1 + \sum_{i=2}^{n} Z_{i,2} X_i$$

This can be expressed more simply as:

$$\bar{G}_2 = \sum_{i=2}^{n} Y_{i,2} X_i$$

– where $Y_{i,j}$ is the net frequency of the breeds in the whole population. If there been no selection in the population, the Y value of any one breed is reduced accord to the total frequency of introductions, but increased by the frequency of introduct of its own breed, such that:

$$Y_{i,j} = Y_{i,(j-1)} (1 - \sum_{i=1}^{n} Z_{i,j}) + Z_{i,j}$$

Y values could be monitored with the aid of genetic markers.
In year 3 there is another introduction of breeds (including the native breed) frequencies $Z_{i,3}$ as described above. However, in this year the value of breed i

$$X_i + \Delta G$$

– where ΔG is the annual selection response in each of the breeds' nucleus units. suming no selection within the population, it follows that:

$$\bar{G}_3 = (1 - \sum_{i=1}^{n} Z_{i,3}) \bar{G}_2 + \sum_{i=1}^{n} Z_{i,3} (X_i + \Delta G)$$

and further:

$$\bar{G}_j = (1 - \sum_{i=1}^{n} Z_{i,j}) \bar{G}_{(j-1)} + \sum_{i=1}^{n} Z_{i,j} (X_i + (j-2) \Delta G)$$

It can be shown that this has a non-iterative equivalent: –

$$\bar{G}_j = X_1 \prod_{m=2}^{j} (1 - \sum_{i=1}^{n} Z_{i,m}) + \sum_{m=2}^{j} \sum_{i=1}^{n} Z_{i,m} X_i \prod_{k=(m+1)}^{j} (1 - \sum_{i=1}^{n} Z_{i,k})$$

$$+ \Delta G \sum_{m=3}^{j} (m-2) \sum_{i=1}^{n} Z_{i,m} \prod_{k=(m+1)}^{j} (1 - \sum_{i=1}^{n} Z_{i,k})$$

The last component of this equation illustrates the genetic improvement due to select effort alone.

It is considered that heterosis and recombination effects between the native br and a novel breed (HNN and RNN respectively) might not be equal or similar to th

Sonderdruck aus Zeitschrift für Tierzüchtung und Züchtungsbiologie
Bd. 97 (1980), H. 2, S. 95-100
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A model for the optimisation of genetic improvement by the introduction of novel breeds into a native population

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Ms. received 30. 9. 1979

Introduction

model is proposed to estimate the long term effects of introducing novel breeds into ative population. The native population (hereafter "the population") is taken as a pulation of animals of one breed, or breed type (the "native breed") which is not der selection but which is commercially farmed or otherwise exploited. It is assumed t all breeds available, including the native breed, are responding equally to selec- n in nucleus units from which introductions can be made. Differences in selection ponse can be taken into account if necessary.

Examples of such a program include:

The introduction of Friesian, Jersey and Brown Swiss cattle into a population of milking *Bos indicus* cattle in a developing country.

The introduction of resistant strains into a wild population of game which is threatened by a disease.

The introduction of fast-growing strains into a lake population of trout.

The model

e subject of improvement can be a single trait or a number of traits in the form of index. Component traits of an index should be considered separately in the mation of both additive and non-additive effects for use in the model.

Consider breeds (i) 1 to n, over years (j) 1 to m. Breed 1 is the native breed. In ar 1, the whole population is of breed 1, and the mean genetic value can be described X_1, where X_i is the "basic value" of breed i under native conditions, (hereafter all antitative values relate to native conditions). Thus, if $\bar{G}_j$ is the mean genetic value the population in year j, we have: $\bar{G}_1 = X_1$

year 2, the novel breeds are introduced in frequencies $Z_{i,j}$, ($i = 2, \ldots, n$; $j = 2$), of *total* population *after* introduction. Z values must be corrected such that they ect the proportion of genes transmitted to future generations from each breed-year roduction group. This requires a knowledge of introduction policy – age and condi- n of introduced animals and their mode of use (group mating, artificial insemination

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Tierzüchtg. Züchtgsbiol. 97 (1980) 95–100

N 0044–3581/ASTM-Coden: ZTZBAS

effects between novel breeds (HNO and RNO respectively), and so these terms are considered separately. Hereafter, the terms "homozygote", "heterozygote", "additive" and "non-additive" refer solely to breed of origin.

The model assumes that genetic equilibrium is instantaneous, or, alternatively, that $\bar{G}_j$ is the mean value of the population when equilibrium has been reached, no introductions having been made between year j and that time. Equilibrium of dominance effects is expected in one generation (or 2 generations if mating is not permitted within breed-year introduction groups). In the absence of genetic linkage, the deviation from equilibrium of recombination effects is halved each generation.

If the use of $Y_{i,j}$ is extended to describe the frequency in the population in year j of genes derived from breed i, then the frequency of homozygotes in year j is:

$$\sum_{i=1}^{n} Y_{i,j}^{\,2}$$

– and conversely the frequency of heterozygotes is:

$$1 - \sum_{i=1}^{n} Y_{i,j}^{\,2}$$

At any one locus, the probability of one gene being "native" and its partner "novel" is:

$$2 Y_{1,j} \, (1 - Y_{1,j})$$

Similarly, the probability of both genes being "novel" but of different breed origin is:

$$1 - \sum_{i=1}^{n} Y_{i,j}^{\,2} - 2 Y_{1,j} \, (1 - Y_{1,j})$$

These probabilities also hold when considering pairs of genes at different loci, and so the non-additive component of $\bar{G}_j$ is:

$$2Y_{1,j}(1-Y_{1,j})(HNN+RNN)+(1-\sum_{i=1}^{n} Y_{i,j}^{\,2} -2Y_{1,j}(1-Y_{1,j}))(HNO+RNO)$$

where HNN and HNO are the values of these effects expected in F_1 crosses of the appropriate breed types, and RNN and RNO represent the maximum possible loss due to recombination effects (which could only be realized if each gene in the genome were derived from a different breed).

Hence:

$$\bar{G}_j = A_j + B_j + C_j$$

– where:

A_j is the "additive" component:

$$A_j = (1 - \sum_{i=1}^{n} Z_{i,j}) \, A_{(j-1)} + \sum_{i=1}^{n} Z_{i,j} \, (X_i + (j-2) \, \Delta G)$$

B_j is the "non-additive" component between the "native" genes and all "novel" genes:

$$B_j = 2 Y_{1,j} \, (1 - Y_{1,j}) \, (HNN + RNN)$$

C_j is the "non-additive" component between all "novel" genes:

$$C_j = (1 - \sum_{i=1}^{n} Y_{i,j}^{\,2} - 2 Y_{1,j} \, (1 - Y_{1,j})) \, (HNO + RNO)$$

Assumptions in the model

I. Matings, other than introductory matings, are at random.
II. No selection within the population. The model can be extended to take account of differences between genotypes in fitness. However, such differences will result in an unstable mean genetic value on termination of a program and this in turn can make objectives complex.
III. Genetic equilibrium is instantaneous.
IV. $\triangle G$, HNN, HNO, RNN and RNO are the same for all breeds or breed combinations that they encompass. The model can be extended to consider any differences if such information is available.

Predicting optimum programs

A computor program was written to simulate the model and to predict the most cost effective introduction program. The objective was taken as maximisation of genetic gain (after consideration of operating costs) on a year to year, or "running optimum" basis. This is not necessarily the same as maximum gain at a target year, or range of years, which requires a different process.

The computor program is designed to select those $Z_{i,2}$ values which maximise the following:

$$(\bar{G}_2 - \bar{G}_1) - P \sum_{i=1}^{n} Z_{i,2} \qquad \ldots(1)$$

– where P is the amount of genetic gain required to justify the cost of replacing the whole population. P can be replaced in expression 1 by a function involving i, Z and j to take account of known differences in the cost of introducing each animal between breeds, between numbers introduced and between years respectively. HILL (1971) describes methods of computing discounted economic returns which can be relevant here.

When expression 1 has been maximised, the corresponding Z values are fixed as optimal. Then, $Z_{i,3}$ values are considered, and so on. Limits to Z values can be defined according to operating capacity.

Results

As an example, consider the introduction of Sussex and Charolais cattle into a population of *Bos indicus* beef cattle in a developing country where conditions are poor. If, for simplicity, $3^1/_2$ year steer mass is taken as the character to be improved, the following parameters might apply:

1. Mean phenotypic value under native conditions in year 2.
   Native breed, $X_1 = 400$ kg
   Sussex, $X_2 = 430$ kg
   Charolais, $X_3 = 440$ kg
2. Selection response per year in nucleus units: $\triangle G = 2$ kg
3. Maximum heterosis: HNN = 60 kg
   HNO = 40 kg

4. Maximum recombination effect: RNN = –12 kg
   RNO = – 8 kg
5. Cost factor: P = 50 kg. Total replacement of the population would have to give a 50 kg improvement to justify costs.
6. Maximum possible introduction in any one year (Z_{max} [total]):
   – If this involves exclusive use of introduced A.I. bulls, and if the generation interval is 5 years then:

$$Z_{max}\ (\text{total}) = \frac{\text{proportion of usage}}{(\text{number of sexes}) \times (\text{generation interval})} = 0.1$$

7. Maximum possible introduction in any year of any one breed:
   $Z_{max} = 0.08$

The results based on these figures are given in the table. In years 2 to 6, the heterosis between native and novel breeds justifies the cost of a high level of introduction of novel breeds into the population. In years 7 and 8, the increase in this source of improvement gained by making further introductions does not justify the cost. However, from year 9 onwards, the added benefit of the cumulating response to selection in the nucleus units justifies a low level of introductions.

Note that $\overline{G}$ and its components are maintained in years 7 and 8 when no introductions are made.

C values are lower than B values for two reasons:

1. In the years shown, the probability of a novel gene being paired with another novel gene of different breed origin is low.
2. The sum of heterotic and recombination effects is lower between novel genes of different breed origin than between novel and native genes.

Predicted optimum introduction program (Z - to the nearest 0.2%), with resulting breed frequencies (Y), mean genetic value ($\overline{G}$), its components (A, B, C) and operating cost

Year (j)	$Z_{1,j}$(%)	$Z_{2,j}$(%)	$Z_{3,j}$(%)	$Y_{1,j}$(%)	$Y_{2,j}$(%)	$Y_{3,j}$(%)	A_j(kg)	B_j(kg)	C_j(kg)	$\overline{G}_j$(kg)	Cost (kg)
1	–	–	–	100.0	0.0	0.0	400.0	0.0	0.0	400.0	–
2	0.0	2.2	7.8	90.0	2.2	7.8	403.8	8.6	0.1	412.5	5.0
3	0.0	2.2	7.8	81.0	4.2	14.8	407.4	14.8	0.4	422.6	5.0
4	0.0	2.2	7.8	72.9	6.0	21.1	410.8	19.0	0.8	430.6	5.0
5	0.0	4.0	6.0	65.6	9.4	25.0	413.9	21.6	1.5	437.1	5.0
6	0.0	4.0	5.8	59.2	12.4	28.4	416.9	23.2	2.3	442.3	4.9
7	0.0	0.0	0.0	59.2	12.4	28.4	416.9	23.2	2.3	442.3	0.0
8	0.0	0.0	0.0	59.2	12.4	28.4	416.9	23.2	2.3	442.3	0.0
9	0.0	1.0	1.0	58.0	13.2	28.8	417.5	23.4	2.4	443.3	1.0
10	0.0	0.8	1.0	57.0	13.8	29.3	418.1	23.5	2.6	444.3	0.9
11	0.0	0.8	1.4	55.7	14.3	30.0	418.9	23.7	2.7	445.4	1.1
12	0.0	0.8	1.0	54.7	14.8	30.5	419.6	23.8	2.9	446.3	0.9
∞	–	–	–	18.1	33.2	48.7	–	–	–	–	–

Summary

A model is proposed to estimate the effects of introducing novel breeds into a native population. Parameters include selection response in nucleus units, heterosis and recombination effects between native and novel breeds and between novel breeds, a cost factor and limits to operating capacity. A computor program was written to simulate the model and to predict the most cost effective introduction program. As an example, a hypothetical case of introducing two European beef cattle breeds into a *Bos indicus* population in a developing country is described. Results are presented and briefly discussed.

Résumé

Un modèle pour optimer l'amélioration génétique par l'import de nouvelles races

Un modèle est proposé pour estimer les effets d'importation de nouvelles races dans les populations indigènes. Des paramètres incluent le succès de sélection dans l'unité du nucleus, l'hétérosis et les effets de recombination entre races nouvelles et indigènes et entre nouvelles races et limites de capacité d'entreprise. Un computerprogramme a été établi pour la simulation du modèle et pour l'estimation des programmes à prix avantageux. Par exemple, on décrit un cas hypothétique d'importation de deux races d'engraissement européenne dans une population *Bos indicus* d'un pays en voie de développement. Les résultats sont présentés et discutés brièvement.

Resumen

Modelo para optimar el mejoramiento genético en el caso de la introducción de nuevas razas

Se propone un modelo para estimar la eficiencia de la introducción de nuevas razas en una población nativa. Los parámetros incluyen: respuesta a la selección en los hatos núcleo, heterosis y efectos de recombinació entre razas autó ctonas y nuevas así como entre las últimas, factor de coste y límites de la capacidad operacional.

Fué elaborado un programa de computadora para simular el modelo y determinar el programa más efectivo en comparación con los gastos.

Como ejemplo se describe el caso hipotético de la introducción de dos razas bovinas europeas de carne en una población de bos indicus. A continuación se discuten brevemente los resultados.

Zusammenfassung

Modell zur Optimierung genetischer Verbesserung durch Einfuhr neuer Rassen

Es wird ein Modell zur Schätzung der Wirkungen der Einfuhr neuer Rassen in einheimische Populationen vorgeschlagen. Parameter beinhalten Selektionserfolg in der Nukleuseinheit, Heterosis und Rekombinationswirkungen zwischen nativer und neuen Rassen, ein Kostenfaktor und Begrenzungen der Unternehmenskapazität. Ein Computerprogramm wurde zur Simulation des Modells und zur Schätzung der kostenwirksamen Programme entwickelt. Als Beispiel wird ein hypothetischer Fall der Einfuhr zwei europäischer Mastrassen in eine *Bos indicus* Population eines Entwicklungslandes beschrieben. Die Resultate werden dargestellt und kurz diskutiert.

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$$\frac{P_A}{P_B} \quad \frac{Q_A}{Q_A} \quad \text{and} \quad \frac{P_A}{P_B} \quad \frac{Q_A}{Q_B}$$

DICKERSON (1972) defines recombination loss as a deviation from linear association with heterosis, such that: "...the coefficient of r^l describes the average fraction of independently segregating pairs of loci in gametes from both parents which are expected to be non-parental combinations". r^l is the maximum possible recombination loss in an individual due to his own genotype – this can only be realised when all genes are derived from a different breed.

DICKERSON (1979) points out that this definition (refered to here as hypothesis Z) is biologically compatable with hypothesis X and that these are related through degree of heterozygosity.

It is not proposed that hypothesis X or Y is universal or even common, but that the underlying situation in a given population can involve both phenomena and other intermediates.

Expected coefficients of maximum epistatic loss (e) under the three hypotheses X, Y and Z are presented in Table 1 for various mating systems. It should be noted that the differences between hypotheses in expected coefficients can be large.

Table 1

Expected coefficients of maximum possible epistatic loss (e) under three hypotheses

2-locus interaction alone is considered, and linkage is assumed to be absent. Equal breed participation and equilibrium are assumed where appropriate (but see footnote)

Mating system	Hypothesis X[1]	Hypothesis Y	Hypothesis Z
2 breed cross $A♂ \times B♀$	1/2	0	0
3 breed cross $A♂ \times BC♀$	5/8	1/4	1/4
4 breed cross $AB♂ \times CD♀$	3/4	1/2	1/2
2 breed synthetic and 2 breed F_2	1/2	1/4	1/2
n breed synthetic	$\frac{n-1}{n}$	$\left(\frac{n-1}{n}\right)^2$	$\frac{n-1}{n}$
2 breed rotation	4/9	1/9	2/9
n breed rotation	$\frac{2(2^n-2)}{3(2^n-1)}$	$(2^n-2)(2^n-1)-\frac{(2^{2n}-4)}{3}$	$\frac{2^n-2}{3(2^n-1)}$
Terminal $♂ \times$ 2 breed rotation ♀	11/18	2/9	2/9
Terminal $♂ \times$ n breed rotation ♀	$3/4-\frac{2^{2n}-1}{12(2^n-1)^2}$	$\frac{2^n-2}{3(2^n-1)}$	$\frac{2^n-2}{3(2^n-1)}$

[1] Alternatively $(1-\sum_1^R p_i^2)$ for all mating systems, where p_i is the proportion of breed i genes expected in the individuals of interest: (Adapted from Dickerson, 1979)

However, discussion of specific types of interaction does not reveal the nature of the underlying situation. A model is required which can describe all types of epistatic interaction. The following are assumed:

1. Genetic linkage is absent.
2. 2-locus epistatic interaction alone is considered.

Table 2

Expected frequencies of the 2-locus configurations $\alpha, \beta_1, \ldots, \gamma_3$, and proportions of individual, maternal and paternal heterosis under various mating systems
Assumptions as in Table 1

Mating system	$f(\alpha)$	$f(\beta_1)$	$f(\beta_2)$	$f(\gamma_1)$	$f(\gamma_2)$	$f(\gamma_3)$	H^I	H^M	H^P
2 breed cross A ♂ × B ♀	0	0	0	1	0	0	1	0	0
3 breed cross A ♂ × BC ♀	0	0	0	1/2	1/2	0	1	1	0
4 breed cross AB ♂ × CD ♀	0	0	0	1/4	1/2	1/4	1	1	1
2 breed synthetic / 2 breed F_2	1/8	1/2	0	1/4	0	0	1/2	$\frac{1/2}{1}$	$\frac{1/2}{1}$
n breed synthetic	$\frac{(n-1)}{n^3}$	$\frac{4(n-1)}{n^3}$	$\frac{2(n-1)(n-2)}{n^3}$	$\frac{2(n-1)}{n^3}$	$\frac{4(n-1)(n-2)}{n^3}$	$\frac{(n-1)(n-2)(n-3)}{n^3}$	$\frac{n-1}{n}$	$\frac{n-1}{n}$	$\frac{n-1}{n}$
2 breed rotation	0	4/9	0	4/9	0	0	2/3	2/3	2/3
n breed rotation	0	$\frac{2(2^n-2)}{(2^n-1)^2}$	0	$\frac{2^{2n}-4}{3(2^n-1)^2}$	$\frac{2^{2n+1}-3.2^{n+2}+16}{3(2^n-1)^2}$	0	$\frac{2^n-2}{2^n-1}$	$\frac{2^n-2}{2^n-1}$	$\frac{2^n-2}{2^n-1}$
Terminal ♂ × 2 breed rotation ♀	0	0	0	5/9	4/9	0	1	2/3	0
Terminal ♂ × n breed rotation ♀	0	0	0	$\frac{2^{2n}-1}{3(2^n-1)^2}$	$\frac{2(2^n-2)}{3(2^n-1)}$	0	1	$\frac{2^n-2}{2^n-1}$	0

H^I – individual heterosis. H^M – maternal heterosis. H^P – paternal heterosis.

3. The term 'heterosis' relates exclusively to intra-locus genetic interactions.
4. For simplicity of illustration, the magnitudes of heterosis and epistatic loss are independent of the specific breeds involved.

No assumption is made that epistatic loss is necessarily a negative effect.

Let the configuration of any 2-locus system be identified by α (homozygote-homozygote), or β_1 or β_2 (homozygote-heterozygote), or γ_1 or γ_2 or γ_3 (heterozygote-heterozygote), such that:

α	represents	$\frac{K}{K}$	$\frac{L}{L}$
β_1	represents	$\frac{K}{K}$	$\frac{L}{K}$
β_2	represents	$\frac{K}{K}$	$\frac{L}{M}$
γ_1	represents	$\frac{K}{L}$	$\frac{K}{L}$
γ_2	represents	$\frac{K}{L}$	$\frac{K}{M}$
γ_3	represents	$\frac{K}{L}$	$\frac{M}{N}$

– where K, L, M and N indicate differences in breed of origin.
For example:

γ_2	also represents	$\frac{N}{L}$	$\frac{M}{N}$

Let $f(\alpha)$, $f(\beta_1)$, ..., $f(\gamma_3)$ represent the expected frequencies of these configurations in individuals of interest. Table 2 presents these frequences under various mating systems. For example, half of all 2-locus pairs in individuals generated by a 3-breed cross are expected to be of configuration γ_1, the remainder being of configuration γ_2.

Let a, b_1, b_2, c_1, c_2, and c_3 represent the proportion of all interactions within the configurations α, β_1,..., γ_3 which are affected by a difference in breed of origin. Table 3 presents the values of a, b_1,..., c_3 under hypotheses X and Y. For example, 3/4 of all pairs of genes chosen at random, one from each locus of a γ_2 configuration are of different breed origin. Referring to hypothesis X, this implies that 3/4 of the dimorphic enzyme molecules will be hybrid.

Any hypothesis about the nature of epistatic loss can be fully described in the same manner as are X and Y in Table 3.

Notice that the product of a 'hypothesis vector' from Table 3 (eg. X: 1, 1/2, 1, 1/2, 3/4, 1) and a 'mating system vector' from Table 2 (eg. terminal ♂ × 2-breed rotation ♀ : 0, 0, 0, 5/9, 4/9, 0) equals the corresponding element in Table 1 (in this case, 11/18).

Table 3

The values of a, b_1,..., c_3 under hypotheses X and Y

See text for details

Hypothesis	a	b_1	b_2	c_1	c_2	c_3
X	1	1/2	1	1/2	3/4	1
Y	1	1/4	1	0	1/2	1

The problem is to find the values of a, $b_1, \ldots, c_3$ which relate to the population and trait of interest. If there are reliable estimates of the mean phenotypic values of individuals generated by a number of mating systems, simultaneous equations can be set up summing the contributions of ae, b_1e, b_2e, c_1e, c_2e, c_3e, individual heterosis, additive genetic effects and maternal and paternal effects (including heterotic and epistatic effects) to these observed values. For example, referring to Table 2, the equation for a 3-breed cross A♂ × BC♀ would be:

$$V = 1/2c_1e + 1/2c_2e + H^I + 1/2G_A + 1/4G_B + 1/4G_C + 1/2M_B + 1/2M_C + H^M + c_I^m e_m + P_A + \text{error}$$

– where V is the observed mean, e is maximum possible epistatic loss due to an individual's genotype, H^I is maximum individual heterosis (as expressed in an F_1 cross), G_A is the mean genetic value of breed A, M_B is the maternal effect of breed B, H^M is the effect on the individual of heterosis in an F_1 dam, c_I^m relates to the maternal trait, e_m is the effect on the individual due to maximum possible epistatic loss in the dam, and P_A is the paternal effect of breed A.

These equations can be expanded to take account of and estimate heterosis and epistatic loss relating to specific breeds. Solution with any degree of accuracy would require a vast body of data. However, the following assumption can be made:

$$a = b_2 = c_3 = 1 \qquad \ldots . 1$$

This is not unreasonable as the configurations α, β_2, and γ_3 involve no within-breed interaction between the two loci. Moreover, it is likely that maternal effects and mean breed genetic values can be estimated more directly elsewhere and included in the equations as constants rather than as variables.

Given expression 1, e can be estimated independently. The resulting estimates of a, $b_1, \ldots, c_3$ can be used as above, to aid in the deterministic evaluation of any complex mating system where $f(\alpha), f(\beta_1), \ldots, f(\gamma_3)$ can be estimated.

In addition, estimated values of a, $b_1, \ldots, c_3$ can be used to make inferences about the nature of epistatic interactions operating in the population.

Of course, no estimates of a, $b_1, \ldots, c_3$ are presently available, but it should be noted that according to this model, heterosis cannot be directly determined from an F_1 cross unless c_1 and/or e can be shown to be sufficiently small. If c_1 and e are significant and e is negative, a direct estimate of heterosis will be an underestimate. Recall that heterosis here relates to intra-locus interactions alone.

TEEHAN *et al* (1979) calculate and express 'recombination loss' as the deviation of the mean of various 3-breed crosses in sheep from the mean of the appropriate 2-breed crosses. This is equivalent to 0.25e (hypothesis Y) or 0.125e (hypothesis X) such that any estimate of e itself can be subject to a two-fold error. Similarly, a two-fold error can be involved when e is calculated from the means of the parental, F_1 and F_2 generations of a 2-breed cross.

Whether one calculates e on the basis of hypothesis X or Y, the data of TEEHAN *et al* (1979) indicate that e is of opposite sign to F_1 heterosis and comparable in magnitude.

Post script: An experiment is underway at Ås to measure the parameters introduced in this paper. This involves four inbred strains of mice in a design which eliminates complications due to additive genetic and maternal effects.

Summary

"Recombination loss" depends on interactions between diploid loci and as such is more complex than "dominance gain" which depends on the singular interactions within loci. A model is proposed to measure the expression and magnitude of recombination loss in terms of four parameters, three of which indicate the nature of gene action involved. Linkage is assumed to be absent and 2-locus interactions alone are considered. Such information will aid in the *a priori* evaluation of complex mating systems.

Résumé

L'expression de la perte de recombination avec caractères quantitatifs.

„Perte de recombination" dépend des interactions entre les loci diploids et est, par conséquent, plus complexe que le „gain de dominance", lequel est basé uniquement sur les interactions en dedans les loci. Un modèle, comprenant quatre paramètres; dont trois drécrivent la nature de l'effet impliqué des gènes, est proposé pour mesurer l'expression et l'étendue des pertes de recombination. On suppose l'absence de linkage et seulement deux locus interactions sont considérées. Une telle information devrait être de grande utilité de la *a priori* évaluation de systèmes d'accouplement complexes.

Resumen

La expresión de la „pérdida de recombinación" en el caso de características cuantitativas

La „pérdida de recombinación" depende de interacciones entre diploides loci y por es más compleja que la „ganancia de dominación" que depende de interacciones singulares dentro de los loci. Se propone un modelo para medir expresión y magnitud de la pérdida de recombinación con cuatro parámetros. Tres de ellos indican la naturaleza de la acción implicada de genes. Suponiendo ausencia de conexión se consideran solamente interacciones 2-locus. Una tal información será útil para la evaluación previa de sistemas de apareamiento complejos.

Zusammenfassung

Formulierung des Rekombinationsverlustes bei quantitativen Merkmalen

„Rekombinationsverlust" hängt von Interaktionen zwischen diploiden Loci ab und ist daher komplexer als der „Dominanzgewinn", welcher lediglich auf Interaktionen innerhalb Loci beruht. Ein Modell wird zur Erfassung der Form und des Umfanges von Rekombinationsverlusten vorgeschlagen, welches vier Parameter umfaßt, wovon drei die Art der implizierten Genwirkung beschreiben. Es wird Abwesenheit von Kopplung angenommen und nur Zwei-Lokusinteraktionen berücksichtigt. Solche Information sollte bei der *a priori* Bewertung komplexer Paarungssysteme von Nutzen sein.

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