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DEMAND FEEDING AND GROWTH IN SALMONIDS.

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SUMMARY.

Rainbow trout of 35 g or more and 1 year old salmon smolts were acclimated to seawater in recirculating systems, or more successfully in floating cages in Dunstaffnage Bay at salinities of 25 ‰ to 30 ‰.

Rainbow trout learnt within 24 h to press a lever to operate an automatic feeder dispensing dry food pellets. They could be trained by an experimenter firing the feeder to cause food deliveries immediately adjacent to the trigger, but would also learn to use the trigger without any training, particularly when in groups rather than as individuals.

Feeds were highly aggregated, bouts of rapid feeding being followed by some hours with very little feeding activity. Feeds within bouts were spaced at a mean of 4 to 8 mins. There was a marked peak of feeding activity at dusk and up to 40 % of a days feeds could occur overnight. Individual rainbow trout may waste up to 50 % of the food that they delivered, but wastage was less marked in groups. In groups of up to 20 trout a single individual was responsible for all of the trigger pressing, though all of the fish present took the food and this reduced the amount wasted. The dominant individual with regard to trigger pressing was also

dominant as regards territory.

The total daily intake of food was dependent on the reward per trigger press, and a delivery of 0.1 to 0.15 % of the aggregate weight of fish present gave the maximum intake with the minimum wastage. This level of intake was greater than that recommended by the food manufacturers for maximum conversion efficiency, but it could be reduced by reducing the reward levels. It is suggested that this could provide a suitable scheme for the operation of demand feeders in fish farming. No improvement in growth rates and conversion efficiency was demonstrated by demand feeding compared to twice daily hand feeding to individual rainbow trout, though there was an improvement in conversion efficiency over once daily hand feeding to groups of trout.

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INTRODUCTION

In rainbow trout farming the cost of food is much the greatest single item of recurring expenditure, being greater than the cost of labour and all additional working expenses put together. It is therefore incumbent on the fish farmer to ensure that the method of feeding is the most efficient that his husbandry techniques will allow.

The food manufacturers help in this by publishing tables of feeding rates for various fish sizes and at various temperatures. They also give recommendations as to the number of feeds per day which should be given, which may vary from 8 to 10 for 40 mm trout to 3 to 4 for 250 mm fish. Automatic delivery of food is well established, particularly for feeding fry (Maitland 1887) but demand feeding awaited the advent of the widespread use of dry pelleted food.

Cheap demand feeders are available to the fish farmer. They use a very simple pendulum action operated by the fish and are claimed to increase food conversion efficiency and growth rates. The present project was concerned with using a more sophisticated demand feeder, which allowed quantification of delivery rates and feeding times to see if demand feeding was more efficient and to determine the best way to use it.

Several workers have trained fish to press a lever to

obtain food for behavioural studies, and have devised an equivalent of a Skinner box used so much with pigeons and rats. Haralson and Bitteman (1950) describe a simple lever for experiments with Tilapia, which was improved later (Longo and Bitteman 1959) by coupling it to a record player cartridge which operated a switching circuit. The same authors (Longo and Bitteman 1963) devised an automatic live worm dispenser and with this system were able to investigate theories of learning as applied to fish compared with, for example, rats. Similarly, Northmore (1968) devised an apparatus to deliver food in suspension in a liquid medium in response to a trigger press by fish, and determined visual thresholds by a stimulus tracking technique. Hogan and Rozin (1962) also published a design for automatic food delivery in response to a trigger press.

These workers were all concerned with using a trigger pressing response as an aid in various behavioural studies, and not with simply feeding as such. Adron (1972) describes an automatic feeder suitable for either timed operation, or with a simple trigger, for demand feeding. This dispenses dry food and is adaptable as regards the size of food particles and the size of reward. I am grateful to Dr Adron for giving me the design of this feeder some time before its publication.

The literature on feeding, growth and conversion efficiency in fish is extensive. The basic questions asked are concerned with the proportion of the diet which is used for basal requirements and the proportion for growth, how growth and food utilisation are affected by temperature, age of the fish, amount fed and what other effects such as hierarchy, daylength and feeding regimes are involved. These questions ramify into considerations of chemical and caloric compositions of food and of fish flesh and these in turn require a knowledge of digestion and absorption rates and efficiency.

Daves (1930, 1931) measured maintenance ratios for plaice fed on wet food and similar data on brown trout were obtained by Pentelow (1939), and Brown (1946 a,b and c, 1951). Brown's investigation was also concerned with the effects of hierarchy, temperature, daylength and crowding. Brown (1957) summarises much of the work to that date and Paleheimo and Dickie (1966 a, b, and c) collate and re-analyse published growth data to identify mathematically defined trends. Philips (1969) reviews literature on growth with a bias to the biochemical considerations.

Jensen (1966) describes the saltwater rearing of salmon and trout in Norway, although in Norway the market is for fish of 750 to 1,500g and trout are not introduced to seawater until they weigh about 100g. Milne (1970) considers a variety of

marine fish and shellfish farming ventures in Scotland, although at that time none of these used floating sea cages such as were used in this work. More general reviews of mariculture encompassing economic as well as biological considerations have been written by Hempel (1970) and Brett et al. (1972). Vincent (1960) demonstrated that brook trout from an established fish farm stock were truly domesticated, in that they were more tame and grew more quickly in rearing troughs than their wild counterparts, but were at a disadvantage in streams both as regards growth rates and survival.

MATERIALS AND METHODS.

Automatic Feeder.

The demand feeder used was designed by Adron (1972) it incorporated a 15,000 μF capacitor which is discharged through the feeder solenoid via relay contacts. This has the advantage that, once the capacitor is discharged, there is very little current flow through the feeder solenoid if the relay is accidentally held on by any fault in the fish tank. The construction and circuit of the feeder is shown

below.

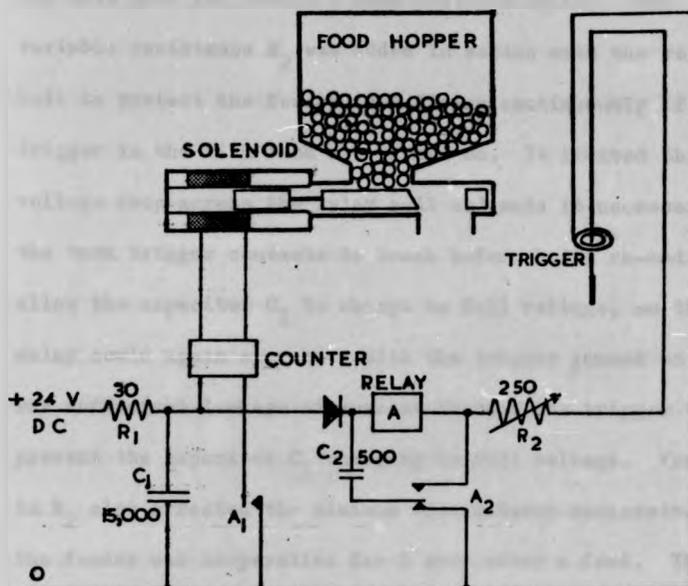


Fig 1. Diagram of the automatic feeder and the circuit used to control it. Resistances are in ohms and capacitances in μF .

Adron's circuit was modified by the addition of a capacitor C_2 connected to changeover contacts on the relay so that it charged up while the relay was relaxed, but this capacitor discharged through the relay coil when the relay was activated. This ensured the relay held on for a minimum time

of about 1 sec no matter how transient the trigger press, and this gave the feeder a very positive action. The variable resistance R_2 was added in series with the relay coil to protect the feeder from firing continuously if the trigger in the fish tank was jammed on. It limited the voltage drop across the relay coil and made it necessary for the tank trigger contacts to break before being re-made, to allow the capacitor C_1 to charge to full voltage, so that the relay could again operate. With the trigger jammed on there was sufficient leakage of current through the trigger to prevent the capacitor C_1 charging to full voltage. Variations in R_2 also affected the minimum time between successive firing; the feeder was inoperative for 3 secs after a feed. This ensured that it could not operate accidentally while the fish were swimming for the food delivered. Adron's design used 15V, but 24V were used in this study to allow more power to be delivered to the feeder solenoids.

The relays had three sets of changeover contacts, of which two were involved in the circuit leaving one set available to trigger an Edgcumbe Peebles 12 pen event recorder which was used to record all feeds, alternatively this third set of contacts could be used to fire an additional relay with a further 4 sets of contacts allowing the synchronous operation of the pen recorder and for example a camera.

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The trigger consisted of a copper washer (size O.B.A.) soldered to a length of brazing rod, and a stainless steel wire passing through the centre of the washer. The end of the wire was protected with P.V.C. sleeving and this the fish pressed in any direction so that the wire made a contact with the washer.

Current flow through the trigger was limited to about 50 mA by the resistance of the relay coil and series resistance R_2 . This was enough to cause considerable corrosion of the contacts if sea water splashed on them, and it was necessary to ensure that the washer was electrically positive so that corrosion took place from the washer rather than from the more delicate wire.

In addition to Adron's design a light operated trigger was used in which the photocell consisted of an integrated circuit light-activated switch (IAS 15. R.S. Components Ltd.), which was connected to a simple external circuit recommended by the manufacturers. The light-activated switch was mounted in a small boiling tube which was sealed with silicone rubber, and a small piece of optic fibre (Crofton plastic light guide) was mounted in front of the switch to reduce the angle of acceptance of light to 70°, and this made the

trigger independent of changes in room lighting.

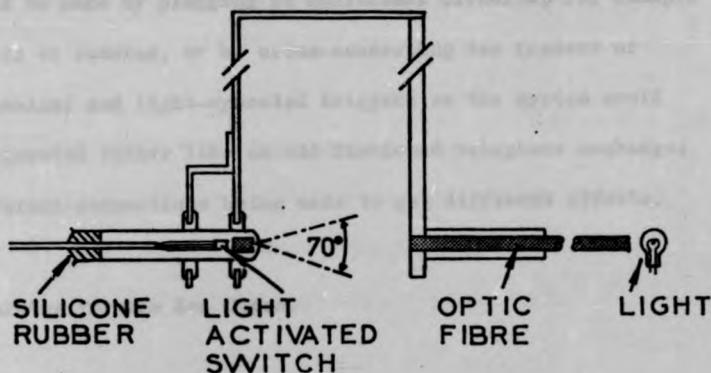


Fig.2. The light operated switch. The fish were required to break the light beam between the light activated switch and the optic fibre.

The light source was a 24V. 2.8W. pilot light which remained outside the tank, the light being transmitted to the switch by a length of optic fibre. The fish were required to break the light beam between the optic fibre and the photocell.

The control circuits were housed in boxes with access by plugs and sockets rather than fixed wires, and this made the system very versatile. Thus changes in experiments could be made by plugging in additional circuits, for example timers or cameras, or by cross-connecting two feeders or mechanical and light-operated triggers so the system could be operated rather like an old fashioned telephone exchange; different connections being made to get different effects.

Apparatus for the Sea Cages.

The feeding apparatus described was used in the Laboratory, but some demand feeding experiments were done in floating sea cages and this required a different approach.

The sea cages were made to a White Fish Authority design and consisted of a substantial floating walkway supporting 4 cages, each 2 m square and 1.3 m deep made of 1.25 cm square mesh of plastic coated wire. The units forming the walkway were hinged together so that they could move with a swell.

The cages were served by a 24 core cable from the laboratory and this provided power at 15 and 24V DC, and enabled information to be conducted back to the laboratory to counters and a pen recorder.

Commercial compressed air operated feeders (Watermill Trout Farm Ltd.) were adapted for demand feeding by substituting solenoid operated air valves for the time clock mechanism. Fig 3 shows the arrangement.

The feeder consisted of an air reservoir which contained air at $2,500 \text{ g/cm}^2$ (35 lbs/ins.^2) from an air bottle supply. At its base was a valve mechanism (A) which was opened by air at $3,500 \text{ g/cm}^2$ (50 lbs/ins.^2) entering through the solenoid valve B. This excess pressure caused a plate to lift in A

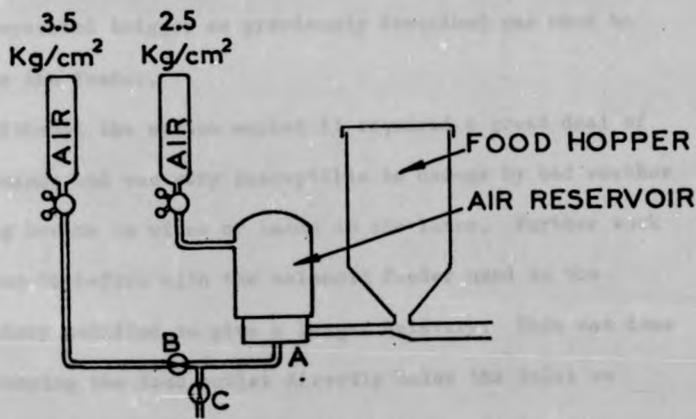


Fig 3. Diagram of the air operated feeders used on the sea cages.

and allowed the air in the reservoir to be vented through the tube at the base of the food hopper. Food fell into this tube by gravity and was shot out with the vented air. It was necessary to have a second solenoid valve (C) which fired about 2 sec after B to release excess pressure in this air line to allow valve A to re-seat itself. The circuit controlling valves B and C is described in the appendix.

While it was necessary to maintain a pressure differential between the two air supplies, both pressures could be raised to increase the range of delivery. At the pressures used food was distributed over 1 to 2 m. A light-operated trigger as previously described was used to operate the feeder.

Although the system worked it required a great deal of maintenance and was very susceptible to damage by bad weather causing breaks in wires or leaks in air lines. Further work was done therefore with the solenoid feeder used in the laboratory modified to give a larger delivery. This was done by arranging the food outlet directly below the inlet so food flowed through as long as the slide remained open. With the original design only 1 'slide full' per shot was delivered. The time for which the slide remained open depended on the value of the capacitors C_1 and C_2 and was about 1 sec using the values shown in Fig 1. The feeder was

mounted in a box with the delivered food being directed down 2.5 cm. plastic piping into the sea cage. The mesh of the cage adjacent to the point of delivery was screened with marine ply to stop food floating out of the cage.

The light operated trigger was also modified in that the sealed boiling tube containing the photocell was mounted on a coil spring directly opposite and adjacent to the optic fibre light source. There was no question of the fish actually breaking the light beam, instead they were required to press the photocell as if it were a lever which moved it out of line with the light source and caused the relay to

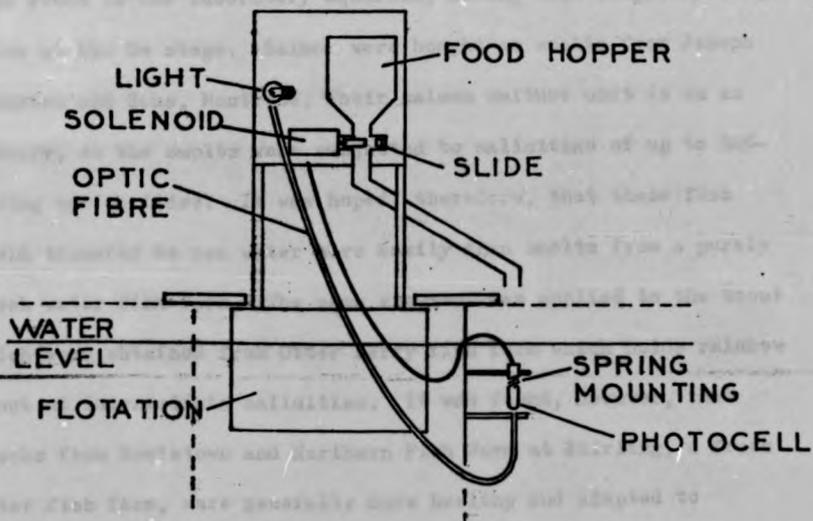


Fig 4. The modified solenoid feeder and light operated trigger used in the sea cages.

operate. The spring mounting ensured an immediate and constant return to the correct position.

This arrangement was preferable for the sea cages since there was no danger of weed or invertebrates breaking the light beam. Since the necessary action is very much a lever pressing response the trigger was more akin to the mechanical trigger used in the laboratory.

Fish Stocks

The fish species used were saithe (Pollachius virens), salmon (Salmo salar) and rainbow trout (Salmo gairdneri), the majority of work being done with rainbow trout. Saithe were kept as a general fish stock in the laboratory aquarium, having been caught by beach seine at the O+ stage. Salmon were bought as smolts from Joseph Johnston and Sons, Montrose. Their salmon culture unit is in an estuary, so the smolts were subjected to salinities of up to 30‰ during spring tides. It was hoped, therefore, that these fish would transfer to sea water more easily than smolts from a purely fresh water fish farm. The same argument was applied to the trout which were obtained from Otter Ferry fish farm which holds rainbow trout at intermediate salinities. It was found, however, that stocks from Howietown and Northern Fish Farm at Stirling, a fresh water fish farm, were generally more healthy and adapted to sea water equally well, so the majority of the stock was eventually purchased from here.

Acclimation to Sea Water

Initial attempts to hold trout in the fresh water supply in the laboratory failed, the trout suffering extensive mortality within the first 24 h. Since the fresh water was not chlorinated this was assumed to be due to dissolved copper (Doudoroff and Katz 1953), particularly since the piping was new. No piped copper-free supply was available. Heavy metal toxicity has the effect of causing gill irritation which leads to excess mucous production and reduction of oxygen interchange. This corresponded to the symptoms observed, although it is appreciated that other toxic materials, for example ammonia, also affect the gills.

A second attempt was made using tap water to which sea water was added to give a salinity of 15‰. The fresh water was left running for a week beforehand to flush out any build-up of copper in the water in the pipes. Although only eight fish were used all eight died within 24 h.

Trout introduced directly into sea water died of osmotic stress within a few days so it was necessary to supply suitable fresh water. Accordingly a successful recirculating system was set up using water collected from a nearby stream, Lusrugan burn at Connel. Such systems are described in detail by Spotte (1970).

The initial filters were constructed in round tanks of 40 cm. diameter and consisted of a supporting mesh of $\frac{1}{4}$ inch netlon covered by a 1 cm. layer of 4-10 mm diam gravel (mean 7 mm.) and a 15 cm. layer of 1-4 mm diam gravel (mean 2.5 mm.), as shown in figure 5. Water was drawn from the fish tank by a centrifugal pump via a funnel screened with $\frac{1}{4}$ inch netlon, so there was no danger of fish being caught on the inlet. It was sprayed onto the top of the filter and drained through the filter and back into the tank.

Two such filters were constructed and used to support two round tanks of 225 l capacity. The filters were initially "conditioned" (i.e. the bacterial flora allowed to stabilise) with only a few fish in the tank, before the final number of fish were added. To guard against the failure of a pump the tanks were cross connected as shown.

The carrying capacity of the filters was calculated from an equation given by Spotte (1970) and the details of these are given in the appendix. It was necessary to hold more fish in the system than the calculated carrying capacity so $\frac{1}{3}$ of the volume of water in the tanks was siphoned off and replaced every 2 days. Either river water or sea water were used to replace the volume siphoned off depending on whether or not it was desired to increase the salinity.

Because of space considerations it was impractical to

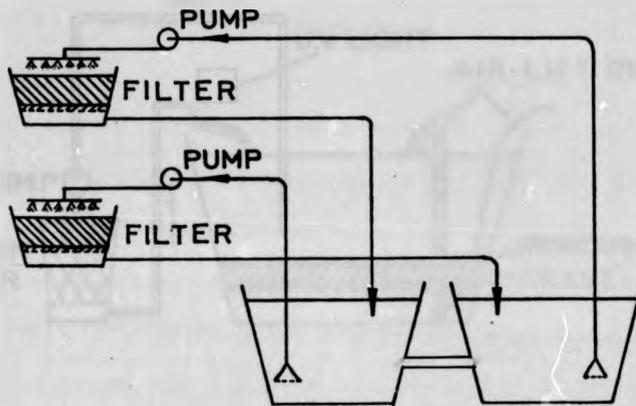


Fig 5. A recirculating system using two percolating gravel filters.

enlarge these filters while using the pumped system.

Consequently the system was later changed by installing a sub-gravel filter in one of the 225 l tanks. A false bottom of netlon plastic mesh was fitted to the tank and covered with a 2 cm deep layer of 4-10 mm diameter gravel, an 8 cm deep layer of 1-4 mm diameter gravel and a 1 cm thick sheet of porous P.V.C. (supplied by Porvair, Kings Lynn, Norfolk). This facilitated the removal of faeces and waste food. Figure 6 shows the arrangement.

Water was recirculated using an airlift pump (Spotte 1970)

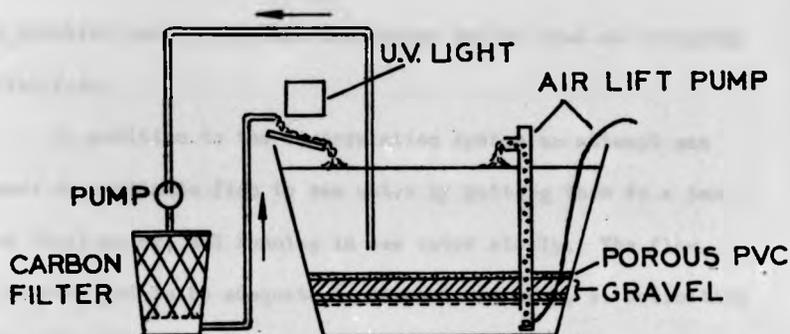


Fig 6. Recirculating system using a sub gravel filter as well as an activated carbon filter and U.V. light to control water quality.

and in addition an Eheim activated charcoal filter was added, the water that had passed through this filter being run over a weir which was irradiated with a 30W. UV light.

This system had a carrying capacity of 10 fish of 40 g each according to the calculations shown in the appendix. It was stocked at this level but as an added precaution half the water was replaced weekly.

With these two systems survival rates were high as long as salinity levels were held below 25‰, but losses after introducing full strength sea water remained high. This was true of the three sources of fish tried, i.e. rainbow trout from a fresh water fish farm, rainbow trout from

a brackish water fish farm and salmon smolts from an estuarine fish farm.

In addition to the recirculation system an attempt was made to acclimate fish to sea water by putting them in a tank of river water, and running in sea water slowly. The flow, however, had to be adequate to support the fish, so salinities rose to 33‰ within three days in a large (1145 l) tank, and one day in a 225 l tank, and this caused too much osmotic stress.

Because of the size of the recirculating system, fish could only be acquired in small groups, so it was common to have only 2 to 5 healthy survivors from each intake. Newly acclimated trout were very susceptible to handling stresses and otherwise healthy fish could die if it was attempted to move them from one tank to another, so the numbers of fish acclimated in the recirculating facilities was necessarily low.

In July 1972 a floating sea cage was installed in Dunstaffnage Bay where salinity levels can fall to 25‰ after heavy rainfall (as measured at a depth of 1.2 m) and it was decided to transfer rainbow trout from freshwater to these cages after a period of rainfall. 108 rainbow trout of about 45 g were put in a cage when the salinity was at 25‰ and the temperature 13.5°C. During the next 10 days the salinity rose slowly to 28‰ and a total of 27 (25%) of the trout died. The rest remained healthy and fed well on a mixture of minced wet

squid and dry pellets, later changed to pellets only. In this way it was possible to acclimate and maintain large numbers of trout in sea water. Two further lots of 300 larger rainbow trout (mean weight 115 g) and 300 smaller rainbow trout of 31 g mean weight were acclimated in the same way. 100 salmon smolts were similarly acclimated though in this case with rather less success. The salmon proved difficult to feed well, so as well as pellets and squid, live food in the form of mysids were also used. Since it was impractical to add mysids to sea cages the salmon were initially acclimated and fed in an aquarium tank and then transferred to a sea cage as soon as possible.

Fish Food.

During acclimation to sea water the fish were fed wet food to reduce their osmotic load. The food was minced squid and dry pellets (1:1) mixed with fresh water and deep frozen. Terramycin was added as a prophylactic in some instances to give dose of 1 mg/kg fish/day.

For the experimental work all the food used was Beta Trout Food manufactured by Coopers Nutrition Products. This is available in either, floating or sinking forms. Rainbow trout however, rarely take sunken food from the bottom so for use in tanks the floating type was used.

The food has the following characteristics (manufacturers information);

Analysis.

Oil	4.0%
Protein	37.0%
Fibre	5.0%
Ash	11.5%
Moisture	10.0%
Carbohydrate (by difference)	32.5%

Vitamins, minerals and trace elements are added.

Sizes.

Grade	For fish of;	Approx partical size.
4	4-5" (10.0-12.5 cm)	2.4-3.5 mm
5	5-7" (12.5-18.0 cm)	3.5-5 mm
6	7-10" (18.0-25.0 cm)	5-7 mm

Sizes 4 and 5 only were used in the automatic feeders because size 6 caused jamming.

Tank Facilities

Individual fish were maintained in white rectangular tanks of 56 l capacity and groups were variously maintained in round black tanks of 225 l, a white rectangular tank of 144 l and round white tanks of 350 and 1145 l. White tanks were easier for observation and cleaning. The tanks were in air conditioned rooms in which the sea water was maintained at 11°C in the summer and ambient (5 to 11°C) in the winter. The largest 1145 l tank was in the general aquarium at ambient temperatures of 5°C in the winter to 15°C in the summer.

In the air conditioned room the water supply entered a strongly aerated header tank then flowed via a funnel full of stones before entering the fish tanks at the water surface. This was to overcome supersaturation in the water which initially caused air embolisms and blindness in the first stocks of saithe held. In the aquarium tank the water was run over a weir before entering the tank for the same reason. In all tanks the flow rates were in the order of one tank volume/5 h and all tanks were also aerated.

Automatic feeders and triggers could be moved from tank to tank, so it was not necessary to move fish about when changing experimental regimes.

Recording of Feeds.

All feeding responses were recorded on a counter and noted daily, and were also, with the exception of initial experiments on saithe, recorded on a pen recorder chart. The chart was run at 7.5 cm/h which allowed feeds within one minute or more of each other to be resolved. Later it was slowed to 1.25 cm/h, when feeds had to be separated by 5 min to be discernable as separate events.

Training to Demand Feed.

Only fish that had been feeding well when hand fed were trained. They were first starved for two days then introduced to the feeder in four ways;

- 1) The feeder was set up with a mechanical (i.e. not light operated) trigger close to the point of delivery of the food. The feeder was fired by an external trigger and the fish observed from the furthest end of the air conditioned room. Characteristically the fish would dash forwards and take the food then retreat from the trigger. Further shots were fired by the experimenter but as the training session proceeded these were delayed until the fish approached the trigger of their own volition, or later in the training session actually touched

it. The feeder was adjusted to give as small a delivery as possible concomitant with it always delivering at least one pellet. In practice this meant an average delivery of 3 or 4 pellets per shot. Training sessions lasted about 30 min and involved the experimenter giving 20 to 30 shots. After this time the fish were generally satiated and less inclined to approach the trigger to take food.

2) Training was automated by arranging for the feeder to fire 4 times at 1 min intervals every 15 min. Again delivery rate was small and was arranged so the pellets fell round the mechanical trigger.

3) Training was ultimately simplified by introducing the feeder and mechanical trigger and giving no training of any sort.

Once fish were trained the mechanical trigger was moved 15 cm from the point where food was delivered so that sea water was not splashed onto the contacts while the food was being taken. In some experiments the trigger was moved 120 cm from the feeder to investigate the effects of such a wide separation.

4) Attempts to train fish to use the light-operated trigger in any of the above three ways were less successful, and it was necessary to first train fish onto the mechanical trigger, then move this closer to the light-operated trigger

until it was almost in the light beam, finally leaving it disconnected for a few days, then removing it. Such training took from 1 to 2 weeks.

Pattern of Feeding.

Information on this came from analysis of the pen recorder charts. A calculator programme was written in which the times of individual feeds (to the nearest minute) were entered, and the programme provided a print-out of the time between any feed and the previous one, the time of the first and last feeds of each day, the number of feeds within 5 min of any other feed, the frequency of occasions when 2, 3, 4, 5 or 5 plus feeds fell within 1 min of each other, the number of feeds within plus or minus 1 hr of dawn and dusk, and the frequency of feeds in each hour of the day. The latter was also plotted as a histogram by an automatic plotter. The results could be expressed as absolute numbers or as a percentage of the total number of feeds entered. Data were usually entered for 10 day periods to allow for the considerable day-to-day variation.

Dawn and dusk were marked on the chart by a photocell connected to a pen and directed towards the window of the air conditioned room. This was set up so that on clear days

it corresponded to civil twilight as given by a Nautical Almanack.

For much of the work the delivery per shot was kept to the low levels used in training so the number of shots was high. Changes in reward level were also made with both individuals and groups of trout to give information on factors controlling feeding patterns as well as to arrive at economical reward levels. Conversely the reward levels could be lowered by introducing a fixed-interval reinforcement schedule with a delivery on only every fifth trigger press. The effect on feeding of giving a number of non-demand feeding shots was investigated by firing the feeder manually, or by a time clock, or by one demand-feeding fish also causing the feeder in another tank to operate. Trout were photographed as they fed, either by a still or cine camera to test for accidental use of the trigger. Room lighting was used for the photography since a flashgun caused too much disturbance. An attempt was made to use infra-red film and a flashgun screened with an infra-red filter, but fast black and white film proved more suitable.

Hierarchy and Territory.

Identification by cold branding was used to elucidate which fish in a group pressed the trigger. Type face was

cooled on solid CO₂ and applied to the anaesthetised trout above and behind the opercula, a dark mark on an otherwise light fish resulting. It was necessary to re-brand the fish every month or so. Groups of from 2 to 23 trout were photographed as the trigger was pressed and a circuit was made which started the cine camera and ran it for 1, 2 or 6 sec when the fish pressed the feeder trigger. Alternatively two still 35 mm cameras were used, one of which wound on automatically and one for which an automatic wind-on system was made.

For studies on territoriality the large rectangular tank (120 x 60 x 20 cm deep) was divided up by $\frac{1}{2}$ inch wire mesh netting barriers which were 12 cm high so the trout could, and did, swim over them, consequently there was no question of a maze being formed. A group of 5 trout were cold-branded for identification. Plots were made of the position of each fish in the tank three times a day. At the same time the feeds were photographically recorded and the feeding fish identified.

Observing territories in branded fish became impractical with larger numbers. In the large aquarium tank (180 cm diameter x 45 cm deep) 23 trout were filmed at periods by an overhead camera both before and after training to use the demand feeder, to see if any aggregation, dispersion or

tendency to group nearer the feeder could be observed. Such observations, as well as film of the feeder triggers, were repeated with 1 and 3 triggers in the tank (all operating the same feeder) to see if individual fish were limited to using one, all or none of the triggers. All filmed records were taken overnight with the aquarium closed, and all films of this and other experiments were supplemented by direct observation.

Growth

Fish were starved for two days prior to weighing, anaesthetised in 1 part per 20,000 M.S. 222 and measured for standard length, fork length and total length. They were blotted dry, using a standard procedure, with two unused paper towels before being weighed in air on a torsion balance. During growth experiments fish were weighed at approximately 3 week intervals.

Because there was considerable variation in growth rate and food conversion efficiency between individuals and between tanks of groups, comparisons between hand and demand feeding were made by alternating trout, or groups of trout, between these two treatments on a 3 week cycle.

Day-to-day food consumption was measured with reference

to the number of deliveries from the calibrated feeder, or over a growing period by the amount added to, and remaining in the feeder.

During periods of hand feeding the trout were fed either once or twice a day either at 0.9.30 or at 09.30 and 16.30. In each case the fish were fed to satiation using a subjective, but as far as was possible, standard measure of satiation, in which feeding was stopped when it was estimated that as many pellets were remaining uneaten as were being eaten. The rate of delivery of food was kept as constant as possible since this affected the amount eaten. Waste was accurately assessed by siphoning off and counting individual uneaten pellets daily, the number of pellets per gram being very constant. The floating pellets were prevented from passing down the overflow by a screen. In one instance, however, a group of fish with a very large reward per trigger press wasted a lot of food and counting pellets was impractical. In this case the overflow screen was removed and waste food collected in a sieve, weighed as wet weight, and this converted to the dry weight by reference to a standard calibration of water uptake by soaked pellets.

It was observed that delivered food was eaten immediately or not at all. If it was not eaten it floated to the sides and stayed there by surface tension. Pellets sank after about 4 h

immersion but maintained their pelleted form for more than 24 h.

RESULTS

Acclimation to sea water.

1. Acclimation using tap water.

Eighty rainbow trout of 50 to 60 g (mean 58.3 g) from Howietown freshwater fish farm at Stirling were put in two tanks with a strong flow of tap water at 12.5°C. Twelve hours later (overnight) many fish started to become unconscious^s but recovered when put in full strength sea water^{as an emergency measure}. Ten hours after this, however, 51 fish were dead and there followed a continuous mortality over the next two weeks. Only two healthy feeding fish adapted to sea water and were used in experiments.

The emergency procedures used did not allow time to mix sea water and tap water, so two lots of 4 trout of the next batch were put in 56 l tanks with a flow of sea^{and}/tap water adjusted to 15% and 12°C. All the fish died within 24 h.

2. Acclimation using river water.

Twenty six rainbow trout of mean weight 55 g were put into the recirculating system described i.e. 225 l tanks containing river water supported by 2 filters of 40 m diameter. Figure

7 shows the results.

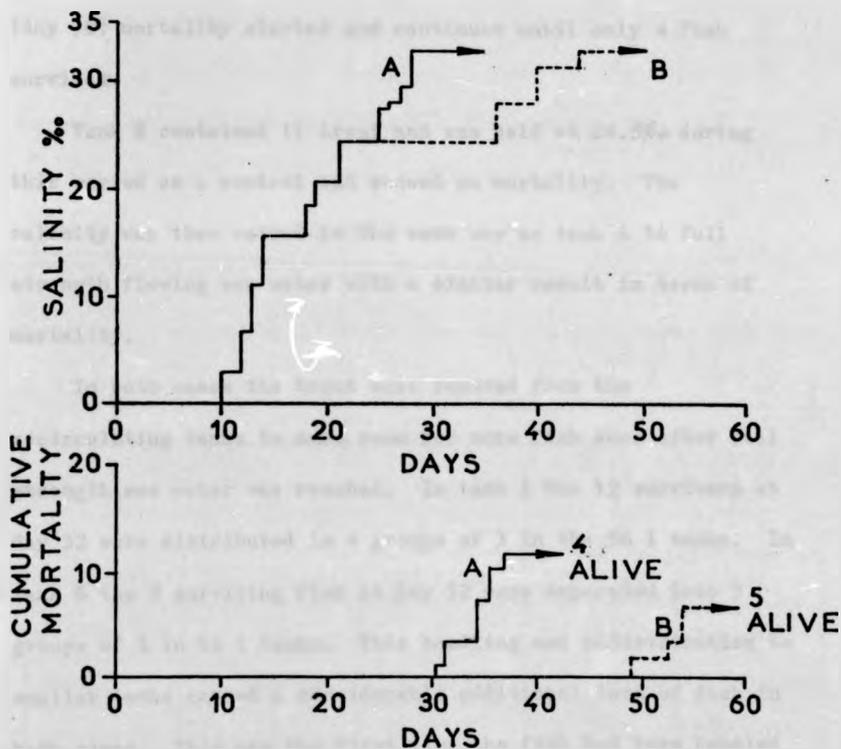


Fig 7. Acclimation to seawater in a recirculating system.

The two tanks were cross-connected until day 25 when the salinity had been raised to 24.5‰ with no mortality. After this the tanks were run independently. Tank A contained 15 rainbow trout and the salinity was further raised to full strength flowing sea water when the recirculation system was

stopped. Once the fish were in full strength sea water (day 30) mortality started and continued until only 4 fish survived.

Tank B contained 11 trout and was held at 24.5‰ during this period as a control and showed no mortality. The salinity was then raised in the same way as tank A to full strength flowing sea water with a similar result in terms of mortality.

In both cases the trout were removed from the recirculating tanks to make room for more fish soon after full strength sea water was reached. In tank A the 12 survivors at day 32 were distributed in 4 groups of 3 in the 56 l tanks. In tank B the 9 surviving fish at day 52 were separated into 3 groups of 3 in 56 l tanks. This handling and redistribution to smaller tanks caused a considerable additional loss of fish in both cases. This was the first time the fish had been handled since their acquisition, the mean weights of the fish during acclimation being calculated from weighing dead trout and not live fish.

Rainbow trout from the brackish water fish farm at Otter Ferry were used next. These had been kept at 22‰ for 2 to 3 months according to the suppliers and were of a mean weight of 21 g. They were acclimated in the sub gravel recirculating system with an initial salinity of 22‰. In addition two lots

of 5 trout were put in similar water without recirculation, but with a trickle feed of sea water at 9°C and 4 trout were put in full strength flowing sea water at 9°C. The results are summarised in Table 1. Survival in all cases was low but was best in the tank with recirculation in which 5 trout were acclimated to sea water.

Table I. Acclimation of trout from the brackish water fish farm.

Treatment:	22‰ Recirc.	22‰ + SW	22‰ + SW	33‰
Initial No.	15	5	5	4
Days	SALINITY ‰ Deaths	SALINITY ‰ Deaths	SALINITY ‰ Deaths	SALINITY ‰ Deaths
1	25 2	24.5 0	26 1	33 0
2	28 2	27.5 2	31 0	33 1
3	33 2	33 2	33 1	33 1
4	33 2	33 0	33 1	33 1
5	33 0	33 0	33 0	33 0
10	33 1	33 0	33 0	33 0
15	33 1	33 1	33 1	33 0
Survivors:	5	0	1	1

A further attempt was made with 40 g trout from Otter Ferry which had been in 27‰. Ten were put in the recirculating 225 l tank at 27‰ and 10 in a 225 l tank also at 27‰ but with no recirculation. Sea water at 9°C was trickled into both tanks. The results are shown in Table 2. Mortality started when full strength sea water was reached and continued for a week leaving only 2 survivors in the recirculating tank and none in the other.

Table 2. Acclimation of 40 g trout from the brackish water fish farm.

Treatment:	Recirculation.		No Recirculation.	
Initial No.	10		10	
Days.	Salinity ‰	Deaths	Salinity ‰	Deaths
0	27.0	0	27.0	0
1	28.0	0	27.0	0
2	29.5	0	29.2	0
3	30.5	2	30.5	1
4	30.5	1	30.5	2
5	30.5	2	30.5	2
6	30.5	2	30.5	0
7	30.5	0	30.5	3
8	30.5	1	30.5	2
9	30.5	0	30.5	0
10	30.5	6	30.5	0
Survivors:	2		0	

Table 5. Acclimation of salmon smolts.

Treatment:	Recirc. Fresh	Fresh ± SW	Sea Water
Initial No:	15	15	18
Days	SALINITY ‰ Deaths	SALINITY ‰ Deaths	SALINITY ‰ Deaths
0	0 0	0 0	31 0
1	0 0	31 0	31 0
2	0 0	31 0	31 0
3	0 0	31 0	31 0
4	15 0	31 0	31 0
5	20 0	31 0	31 0
6	23 0	31 0	31 4
7	26 0	31 6	31 0
8	28 0	31 0	31 0
9	31 1	31 1	31 0
12	31 0	31 2	31 6
15	31 4	31 0	31 2
18	31 8	31 3	31 1
21	31 0	31 0	31 1
24	31 0	31 2	31 3
27	31 0	31 0	31 0
30	31 2	31 0	31 0
Survivors:	0	1	1

A final attempt to acclimatise fish to sea water in the laboratory was made with salmon smolts. On arrival at the laboratory the smolts were separated into 3 tanks;

1. 15 smolts in recirculating river water.
2. 15 smolts in static river water with sea water at 11.5°C trickled in.
3. 18 smolts directly into sea water with a generous flow of sea water.

After 3 days to settle down the salinity in the recirculating system was raised to 31‰ (flowing sea water) over 6 days. As Table 3 shows there was no mortality in this tank for the first 8 days but soon after this all but two of the smolts died and the final two died a few days later.

Results were generally similar with the other two tanks with 1 smolt surviving in each case. Unlike the trout it was difficult to get the salmon to start feeding. The smolts had been fed on pellets at Montrose and this was tried (using the same make of pellets), also chopped and minced squid and live food in the form of mysids. The poor feeding, however, undoubtedly aggravated the mortality.

3. Acclimation using sea cages.

In July 1972 108 rainbow trout of mean weight 35 g were transported from the freshwater fish farm at Stirling to the

sea cage. The salinity at the bottom of the sea cage (1.2 m deep) was 25.2‰, and the temperature 13.5°C. The polythene bags containing the fish were floated on the cage surface for 1 h to allow temperature equilibration, then emptied into the sea cage. The results as shown by Table 4 were a relatively small initial mortality and a survival of 75%. The salinity throughout the period remained below 28.1‰, due to continued rainfall. No significant mortality was observed after the 10 day period covered in Table 4.

Table 4. Acclimation of 35 g trout in a sea cage.

Initial No.	108	
Days	Salinity ‰	Deaths
0	25.2	0
1	25.2	0
2	25.8	0
3	25.0	4
4	28.3	12
5	28.0	2
6	26.3	3
7	25.0	0
8	28.1	4
9	28.0	2
10	27.4	0
Survivors:		61 = 75%

The trout fed well on a mixture of squid and pellets (1:1) plus terramycin added to give 1 mg activity/kg fish/day as a prophylactic. At day 13 the diet was changed to dry pellets only. One month after acclimatisation 45 of these trout were removed from the cage, transported in aerated bins to the laboratory, anaesthetised, weighed, measured and put in an aquarium tank without any further mortality, hence acclimation was complete.

A further group of 270 rainbow trout from freshwater were similarly acclimated. At 115 g mean weight these fish were much larger and in this case the initial salinity was higher, 30.1‰ at 12.8°C, but fell a little as acclimation proceeded. The results are summarised below in Table 5. The majority of the mortality was in the first 8 days and survival was 86%.

The final group of rainbow trout were acclimatised in what it was hoped would be particularly suitable conditions of lower water temperature in November, and a very high rainfall, hence much reduced salinity. 300 trout of mean weight 31 g were again brought from Howietown, Stirling and put in a sea cage. The initial salinity was 24.7‰ at 8.4°C as Table 6 shows mortality was low, the survival rate being 93%.

The trout were fed pellets only, but these were soaked in freshwater for the first three weeks after acclimatisation. The windy weather which made access unwise on day 5 and 6 did

Initial No. 270		
Days:	Salinity ‰	Deaths.
0	30.1	0
1	30.1	3
2	28.4	8
3	29.4	0
4	29.7	0
5	30.2	12
6	30.3	0
7	32.0	4
8	31.8	7
9		0
12		0
15		1
18		2
21		0
Survivors:		233 = 86%

Initial No. 300			
Days.	Salinity ‰	Deaths.	Notes.
0	24.7	0	
1	25.1	0	
2	25.3	5	
3	25.0	0	Windy.
4	24.7	7	Stormy.
5)	
6)	Wind prevented access.
7	25.2	10	
8	25.2	0	
9		0	
12		0	
Survivors:		280 = 93%	

Table 5. Acclimation of 115 g trout in a sea cage at

30.1 ‰

Table 6. Acclimation of 300 rainbow trout of 31 g in

a sea cage at 24.7 ‰

Initial No. 270		
Days:	Salinity ‰	Deaths.
0	30.1	0
1	30.1	3
2	28.4	8
3	29.4	0
4	29.7	0
5	30.2	12
6	30.3	0
7	32.0	4
8	31.8	7
9		0
12		0
15		1
18		2
21		0
Survivors:		235 = 86%

Initial No. 300			
Days.	Salinity ‰	Deaths.	Notes.
0	24.7	0	
1	25.1	0	
2	25.3	3	
3	25.0	0	Stormy.
4	24.7	7	Stormy.
5)	
6)	Wind prevented access.
7	25.2	10	
8	25.2	0	
9		0	
12		0	
Survivors:		280 = 93%	

not appear to have any drastic effect on the trout. There was no further mortality as salinity rose after the initial period of acclimation.

An intake of salmon smolts were acclimated in a sea cage in July 1972. Because of the previous difficulty in getting smolts to feed the fish were put in a large aquarium tank (1145 l) which was stocked with a large number of mysids. The tank was initially filled with river water, and sea water at 14.5°C was run in after the fish were introduced. As the salinity reached that of the sea (33‰) half of the smolts were transferred to a sea cage. A few days after this it was apparent that the smolts in the sea cage were doing better than those in the tank so the remaining fish were transferred to the sea cage. Table 7 summarises the procedure and results.

The limited success of this venture was due in part to the large amount of handling involved since each transfer to the sea cages was followed by an appreciable number of deaths, but also to the lateness of the year. By July the natural smoltification was over and the seawater temperatures were rather high. March or April would be a more appropriate time of the year.

Days	Tank			Cage	
	SALINITY %	Deaths.	Survivors.	Deaths.	Survivors.
0	0	0	108		
1	27.5	1	107		
2	29.0	1	106		
3	33.0	11	95		
			50 to cage	→	50
4	33.0	0	45	8	42
5	33.0	2	45	4	38
6	33.0	5	38	2	36
7	33.0	6	32	1	35
8	33.0	7	25	1	34
			25 to cage	→	59
9				12	47
12				5	42
15				6	36
18				3	33
21				0	
Survivors:				33 = 31%	

Table 7. Procedure and results for acclimating salmon smolts to sea water.

Training to Demand Feed.

1. Use of the mechanical trigger.

Figure 8 shows the rates at which individual rainbow trout learnt to use the mechanical trigger to demand feed.

MEAN No FEEDS
PER g FISH WT
PER DAY

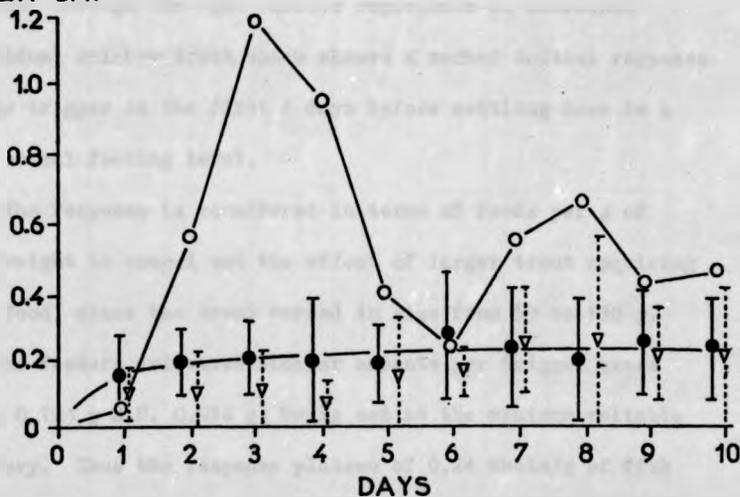


Fig 8. Rate of learning to demand feed by individual rainbow trout. The means and standard deviations for 7 trained trout (closed circles), 5 untrained trout (triangles) and a single untrained individual (open circles).

The trout actively trained by the experimenter (closed circles) started to feed within 24 h and then continued at normal feeding levels. Because of the variation between individuals there was no demonstrable significant difference between the responses of the trained and untrained (triangles) trout. The untrained trout, however, appeared to feed at a generally lower level for the first 6 days after which the feeding rate became very similar to the trained trout. The line through the open circles represents an untrained individual rainbow trout which showed a marked initial response to the trigger in the first 4 days before settling down to a more normal feeding level.

The response is considered in terms of feeds per g of fish weight to cancel out the effect of larger trout requiring more food, since the trout varied in size from 59 to 130 g. All the feeders delivered similar amounts per trigger press (mean 0.124 g S.D. 0.016 g) being set at the minimum reliable delivery. Thus the response plateau of 0.24 shots/g of fish weight corresponded to a delivery of 2.97% of the body weight per day.

The responses in terms of the actual number of trigger presses are given in Tables 8 and 9. The top part of the table summarises the feeding over the 10 days after

Individual:	A	B	C	D	E	F	G
Weight:	63g	66g	66g	69g	96g	112g	195g
Days	Feeds	Feeds	Feeds	Feeds	Feeds	Feeds	Feeds
0	4	17	6	15	21	11	57
1	15	0	12	22	14	54	26
2	4	22	5	15	19	14	65
3	9	15	4	8	38	25	73
4	2	16	2	4	27	45	104
5	5	15	10	6	18	27	99
6	8	10	12	0	40	47	112
7	12	11	1	0	35	56	107
8	4	9	5	2	24	51	119
9	off	2	off	9	27	45	97
10	off	9	off	4	27	27	95
First Day							
Hours							
2	0	0	0	1	0	2	0
4	0	0	0	1	0	15	0
6	0	0	0	2	0	1	0
8	0	0	8	5	0	1	0
10	8	0	1	5	0	2	7
12	1	0	2	0	0	6	5
14	5	0	0	2	0	5	0
16	0	0	0	0	1	2	6
18	0	0	0	2	5	2	7
20	1	0	1	2	4	0	5
22	0	0	0	5	2	0	0
24	0	0	0	1	4	0	0

Table 8. Initial demand feeding shots by trained individual rainbow trout. All feeds on day 0 are training shots. The bottom half of the table gives more details of the first days demand feeding.

Individual:	A	B	C	D	E	F	G
Weight:	63g	66g	66g	69g	96g	112g	195g
Days	Feeds	Feeds	Feeds	Feeds	Feeds	Feeds	Feeds
0	4	17	6	15	21	11	57
1	15	0	12	22	14	54	26
2	4	22	5	15	19	14	65
3	9	15	4	8	38	25	73
4	2	16	2	4	27	43	104
5	5	15	10	6	18	27	99
6	8	10	12	0	40	47	112
7	12	11	1	0	35	56	107
8	4	9	3	2	24	51	119
9	off	2	off	9	27	43	97
10	off	9	off	4	27	27	93
First Day							
Hours							
2	0	0	0	1	0	2	0
4	0	0	0	1	0	15	0
6	0	0	0	2	0	1	0
8	0	0	8	3	0	1	0
10	8	0	1	5	0	2	7
12	1	0	2	0	0	6	3
14	3	0	0	2	0	5	0
16	0	0	0	0	1	2	6
18	0	0	0	2	3	2	7
20	1	0	1	2	4	0	3
22	0	0	0	3	2	0	0
24	0	0	0	1	4	0	0

Table 9. Initial demand feeding shots by untrained rainbow trout.

Individual:	H	I	J	K	L
Weight:	59g	68g	97g	130g	132g
Days	Feeds	Feeds	Feeds	Feeds	Feeds
0	0	0	0	0	0
1	4	15	11	4	3
2	3	4	35	5	12
3	5	13	30	1	0
4	11	2	7	1	2
5	26	12	7	2	0
6	14	16	25	13	9
7	26	11	12	52	14
8	46	0	18	35	0
9	20	10	40	23	1
10	33	5	20	25	2
First Day					
Hours					
2	no data	6	1	3	1
4	no data	1	0	0	1
6		0	2	0	0
8		6	0	0	0
10		2	2	0	0
12		0	0	0	0
14		0	0	0	0
16		0	0	0	0
18		0	3	0	1
20		0	0	0	0
22		0	2	0	0
24		0	1	1	0

introducing the feeder, and the bottom part shows in more detail the feeding during the first 24 h of this period.

Demand feeding started within the first few hours after introducing the feeder and this was more marked in the trout which were not trained. This apparent improvement in learning rate was due to the untrained trout being more hungry. All the fish were starved for 2 days before introducing the feeder but the trained fish received some food during the training session and hence were less hungry for the first day.

In two cases groups of rainbow trout were established and the feeder introduced within a few days but without any training. In both cases the feeding response was poor as shown in Table 10. This was due to the considerable antagonistic behaviour involved when small numbers of rainbow trout were put in the same tank. This was manifest in the tank of 3 trout in which only 1 was left alive after 5 days.

To overcome this, only well established groups were used and tanks were very loosely divided up with $\frac{1}{2}$ inch wire mesh divisions to allow territoriality without excessive interaction. The learning rate in such groups is shown in Table 11. The group of 58 trout shown in Table 11 were not in a tank but were in a floating sea cage and this was not divided up in any way.

Table 10. Poor initial response to feeder by newly established untrained groups of rainbow trout.

No. in group.	5	5
No. of days established:	0	4
Days.	Feeds	Feeds
0	0	0
1	0	3
2	2	1
3	fault	0
4	4	0
5	0	0
6	1	0
7	2	0
8	2	6
9	2	0
10	0	1
11	off	2
12	"	5
13	"	8
14	"	0
15	"	7

Table 11. Initial feeding by weal established untrained groups of rainbow trout.

No. in Group:	8	16	23	25	58
Mean Weight:	89g	158g	89g	42g	279g
Days	Feeds	Feeds	Feeds	Feeds	Feeds
0	0	0	0	0	0
1	32	79	22	38	170
2	65	71	23	4	23
3	fault	54	8	4	179
4	30	64	106	4	128
5	96	108	173	3	91
6	fault	121	64	6	50
7	65	28	63	1	261
8	11	140	71	0	197
9	36	fault	182	6	150
10	102	fault	50	8	227
First Day					
Hours					
2	0	1	0	0	90
4	0	2	0	0	2
6	1	14	1	6	0
8	0	12	10	0	0
10	2	10	1	14	0
12	5	1	1	11	0
14	0	1	4	1	0
16	4	12	0	0	76
18	0	19	1	2	4
20	10	6	4	3	0
22	4	3	0	0	0
24	6	8	0	1	0

As with individual trout the fish were recording trigger presses within the first few hours, and, with the exception of the group of 25 trout, settled down to a plateau level within 2 days. This is shown in Fig 9 which is from the combined results of the groups of 8, 16 and 23 trout and is based on the number of shots per g of the total fish weight in the tanks. It shows a similar form to Fig 8.

MEAN No FEEDS
PER g FISH WT
PER DAY

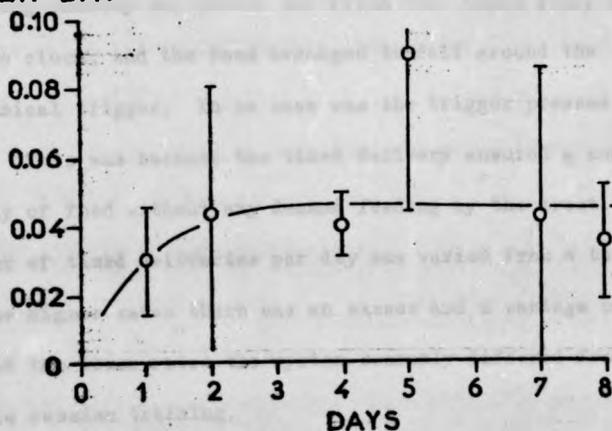


Fig 9. Initial feeding by established untrained groups of rainbow trout. The means and 95% confidence limits from three groups.

As before, the delivery per trigger press was minimised and was similar in all groups (mean 0.124 g S.D. 0.026 g) so the plateau level of 0.045 presses/g fish weight gave a daily food delivery of 0.56% of the weight of fish in the tank. This was lower than that obtained for individual trout (2.97% of the body weight per day). The water temperatures were similar (10-11°C) and the size ranges of the trout involved were also comparable, so this was a real effect due to the grouping of the trout.

An attempt was made with four individual trout to automate training whereby the feeder was fired four times every hour on a time clock, and the food arranged to fall around the mechanical trigger. In no case was the trigger pressed by the fish. This was because the timed delivery ensured a constant supply of food without any demand feeding by the trout. The number of timed deliveries per day was varied from 4 to 36. At the higher rates there was an excess and a wastage of food and at the lower rates the system scarcely differed from single session training.

2. Use of the light-operated trigger.

Two initial attempts were made to train naive trout to use the light-operated trigger directly. A light trigger was introduced to a tank of 6 trout with no training given. After

1 day, there being no response, the feeder was fired externally so food fell beside the trigger for training, but this was still not successful in starting the fish to demand feed. An individual trout was similarly treated, the procedure being more extended with 2 training sessions separated by 5 days and with periodic hand feeding to maintain the fish. Again it did not learn to use the light trigger. In both cases the trout subsequently learned to use a mechanical trigger.

A similar procedure was tried with a group of 19 trained trout which had been demand feeding for some time using a mechanical trigger. This was removed and replaced by a light trigger which the trout operated. The feeding rate was, however, enhanced by a period of 5 days during which the mechanical trigger was re-introduced and moved towards the centre of the light trigger over the 5 day period before being removed. Table 12 demonstrates this.

It was intended to film the trout as they used the trigger to see if this increased use of the light operated trigger was due to one fish firing the trigger more often, or to more trout learning to use it. The group of trout, however, succumbed to an aquarium water failure before this could be done. It was observed that trout tried to press various parts of the light trigger during the initial 16 day period, much as they pressed a mechanical trigger. After the 5 day period

Table 12. An improvement in the use of the light operated trigger after an "instructional" period in which a mechanical trigger was placed adjacent to the light one.

Treatment:	Days.	Mean No. Feeds/Day	Total.
Light trigger only.	16	10.0	10.0
Light and mechanical triggers	5	(Light) 12.2 (Mechanical) 16.4	28.6
light trigger only.	10	33.0	33.0

with both triggers present the trout were more frequently observed to either swim right through the centre of the light trigger in order to break the light beam, or to merely put their head into it, so the period with both triggers present was an effective instructional period.

Subsequent experiments, using the technique of training fish onto the light trigger by means of the mechanical trigger, achieved a smooth transition from one to the other and are

Table 13. Training to use the light operated trigger
by moving a mechanical trigger progressively
closer to it.

No. of Trout.	1		1		1		30	
Mean Weight.	575g		120g		203g		81g	
Days.	M	cm. L	M	cm. L	M	cm. L	M	cm. L
0	34	(8) 0	35	(8) 0	3	(0) 0	0	(0) 0
1	2	0	23	0	6	(0) 0	24	(0) 0
2	0	0	23	(5) 0	-	fault.	-	114
3	0	0	29	0	-	4	-	61
4	75	0	34	(0) 8	-	17	-	89
5	0	(5) 0	-	36	-	20	-	39
6	0	0	-	15	-	25	-	47
7	2	0	-	17	-	25	-	off
8	0	0	-	49	-	26	-	"
9	45	(2) 6	-	22	-	39	-	"
10	56	(0) 1	-	35	-	60	-	"
11	-	4	-	20	-	off.	-	"
12	-	54	-	fault.	-	off.	-	"

M Feeds using the mechanical trigger.

L Feeds using the light trigger.

cm Distance between the two in cm.

detailed in Table 13.

On the first occasion using a large (575 g) trout the changeover period was 11 days, but the technique was equally successful when this was reduced to 5 days in the case of the 120 g trout. With another trout the light trigger was introduced immediately adjacent to the mechanical trigger at the outset, with only a 2 day changeover period and again this was successful. These three individuals had all been demand feeding with the mechanical trigger for some time. A group of 30 naive trout was then established and the mechanical and light-operated trigger introduced at the same time and close together. The mechanical trigger was removed after the first days demand feeding and the trout continued to use the light trigger. A water failure on day 7 killed these fish. It was attempted to similarly train three individual trout to the light and mechanical triggers at the same time, but without success. The trout seemed reluctant to approach the mechanical trigger when it was surrounded by the light trigger and did not, as a consequence, start to demand-feed. After 5 days both triggers were removed and the fish hand-fed for a week, the mechanical trigger only was then re-introduced and all 3 trout learned to use this within 2 days.

Training Fish Other Than Rainbow Trout

Both saithe (Pollachius virens) and salmon (Salma salar) were trained to demand feed. Cod (Gadus morhua) were tried but were found to be unsuitable since they would not take dry pelleted food, this was also true of some wild caught sea trout (Salmo trutta) which adapted very poorly from a changeover of wet to dry food.

Two individuals and two groups of salmon were trained as well as one group of 5 saithe. Active training was only given to 1 salmon and to the saithe, the other salmon demand fed without any training. The mechanical trigger was used in all cases. Table 14, which is comparable to Tables 8, 9 and 11 for rainbow trout, gives the details.

Individual salmon, and the saithe learnt quickly and continued to demand feed. The two groups of salmon, although they learnt to demand feed, continued to feed less well. The rates of learning in these two species were similar to those for rainbow trout. The saithe fed well when hand-fed on dry pelleted food and so made good subjects for demand feeding. The salmon did not feed so well, and there was some difficulty in establishing individuals and groups of salmon which responded to hand feeding actively enough to make experiments on learning to demand feed meaningful.

Table 14. Initial use of the trigger by salmon and saithe.

Species:	Salmon	Salmon	Salmon	Salmon	Saithe
No.of fish:	1	1	3	3	5
Mean wt g :	37	90	39	51	39
Training shots:	11	0	0	0	32
Days: 1	3	44	4	3	10
2	7	12	4	0	0
3	2	52	3	0	13
4	2	fault	1	4	fault
5	3	149	1	7	fault
6	13	71	1	0	3
7	14	26	1	0	40
8	7	21	0	0	7
9	10	20	0	0	20
10	fault	fault	fault	2	24
First 24 hours					
Hours 2	0	0	1	0	no data
4	1	0	1	0	
6	0	4	1	0	
8	0	10	0	1	
10	0	14	0	0	
12	0	3	0	0	
14	2	3	0	1	
16	0	2	0	0	
18	0	2	1	1	
20	0	0	0	0	
22	0	2	0	0	
24	0	0	0	0	

One salmon was further trained to use the light-operated trigger by moving the mechanical trigger towards it over a period of 6 days.

Memory.

Trout which had been demand feeding using the mechanical trigger were hand fed for a period of one or two months, the trigger being removed during this period to avoid extinction of the trigger pressing response. The trigger was then replaced with no re-training and demand feeding re-started. The trout were starved for 2 days prior to re-introduction to the trigger as they had been when initially introduced to it. Fig 10 shows the mean number of feeds per h during the first day after re-introducing the trigger.

The initial response for the first 2 h was similar in all cases, but this was followed by an enhancement of feeding activity in those trout which had had experience of demand feeding. Figure 11 is taken from the pen recorder chart and shows the initial feeding responses of the 6 trout which had been suspended from hand feeding for 1 month. It is evident that most of these fish re-started demand feeding within half an hour of introducing the feeders.

It is not valid to make a comparison with the demand feeding activities of newly trained trout, since the

MEAN No FEEDS
PER g FISH WT
PER HOUR

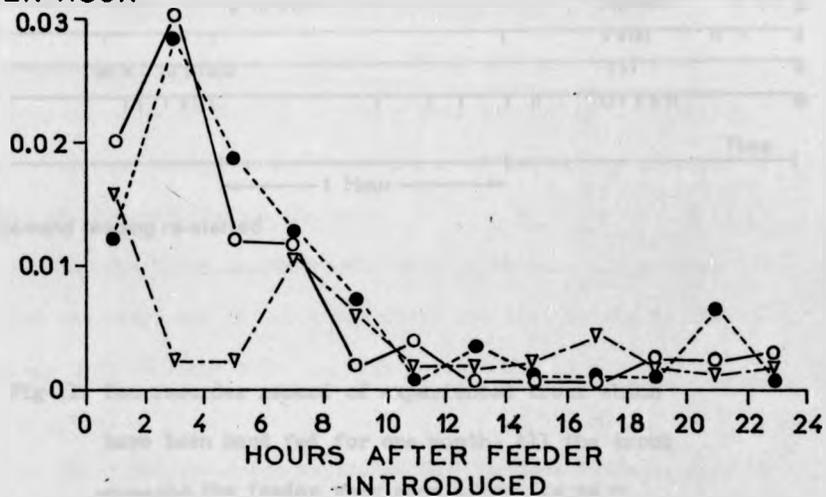


Fig 10. Triangles, mean responses of 4 naive, untrained trout.

Open circles, mean responses of 6 trout experienced in demand feeding but which had been hand fed for 1 month.

Closed circles, 2 experienced trout which had been hand fed for 2 months.

The trout which have had experience of demand feeding show an enhanced response over naive trout.

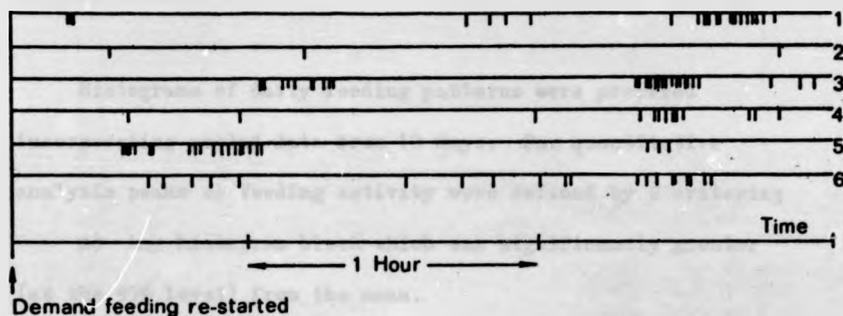


Fig 11. Pen recorder record of experienced trout which have been hand fed for one month. All the trout operated the feeder very soon after its re-introduction.

training involves feeding the trout. This means that they are not similarly starved and this has a marked influence on the rate of intake. (Brett 1971).

Pattern of Feeding.

Diurnal Variation.

Histograms of daily feeding patterns were prepared incorporating pooled data from 10 days. For quantitative analysis peaks of feeding activity were defined by 2 criteria;

A) Any histogram block which was significantly greater (at the 95% level) from the mean.

B) Any block or group of blocks which were all greater than the mean, and in which the first and last blocks in the group were at least twice as high as adjacent blocks outside the group.

The first criterion separated out the more obvious peaks of feeding, but failed to indicate peaks which were relatively low, but which were nevertheless bounded by troughs of feeding activity. Such peaks appeared to occur predominantly at dawn and were defined by the second criterion. Figure 12 shows a number of the histograms obtained.

The median time of the peaks were calculated and plotted against sunrise or sunset as appropriate. There was no significant correlation between feeding activity and dawn. Such dawn peaks as are observed in the histograms appear to represent the first feed of the day, and there is no demonstrable

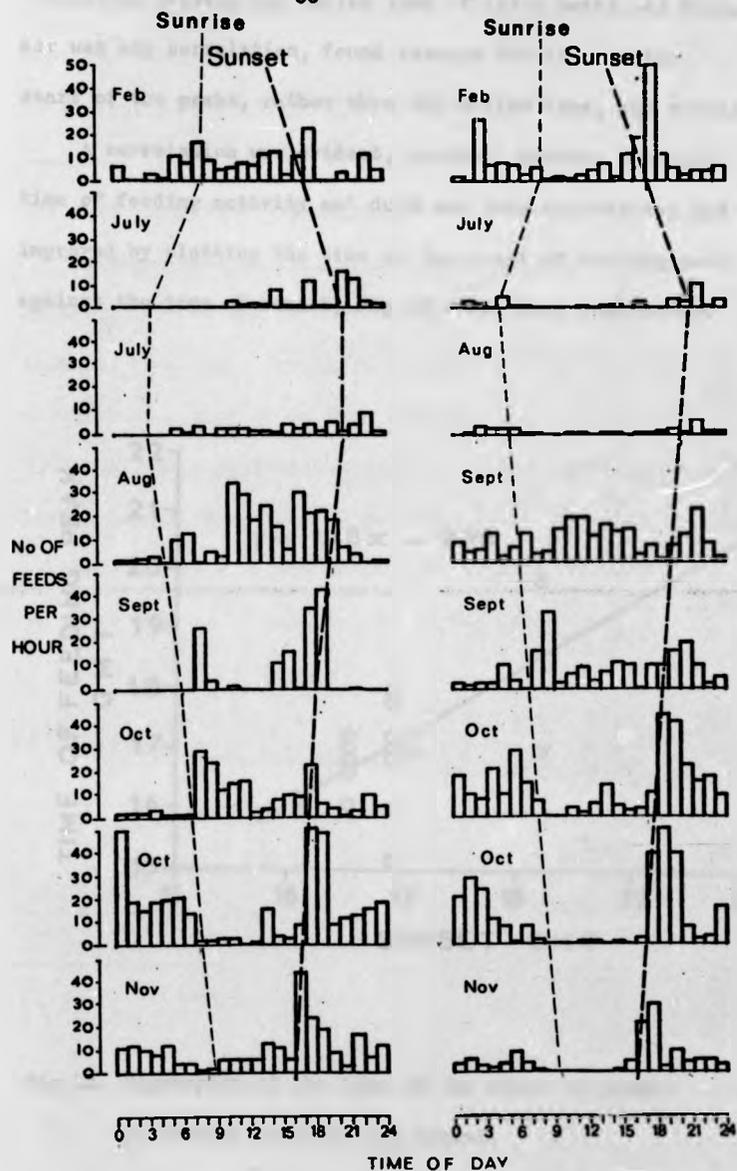
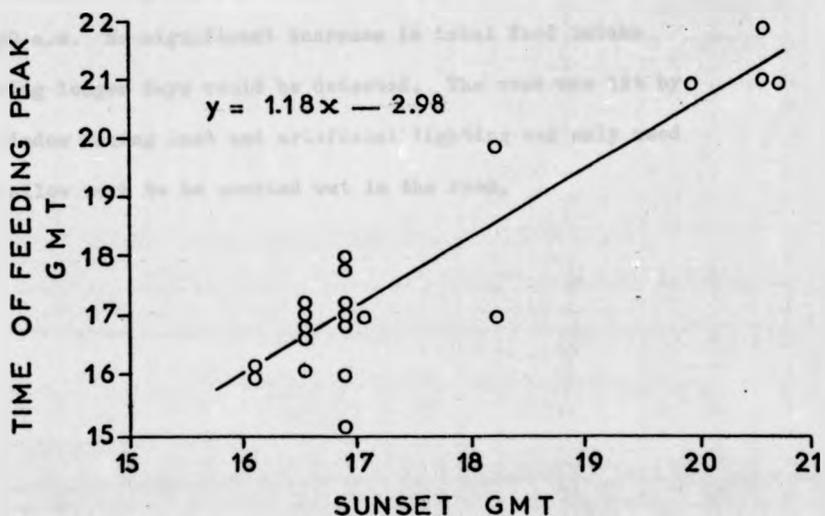


Fig 12. Typical histograms of daily feeding patterns drawn from a total of 5 individual rainbow trout.

connection between the median time of these peaks and dawn, nor was any correlation, found between the time of the start of the peaks, rather than the median time, and sunrise.

A correlation was evident, however, between the median time of feeding activity and dusk and this correlation was improved by plotting the time of the start of feeding peaks against the time of sunset, Fig 13 shows this regression.



The regression was significant at a probability level of 0.01 for the median time of the peaks, but this was improved to a level of 0.001 when the starting time of the peak was used, so feeding started in relation to dusk and continued for a variable time thereafter.

A high level of feeding occurred overnight on many occasions, up to 40% of the total food delivery being between dusk and dawn (civil twilight to civil twilight), often with a conspicuous peak of feeding activity between midnight and 3.00 a.m. No significant increase in total food intake during longer days could be detected. The room was lit by a window facing East and artificial lighting was only used to allow work to be carried out in the room.

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Aggregation of Feeds

A striking feature of the pen recorder charts was the way in which feeds were aggregated into bouts of activity as shown below by a photocopy of a section of the pen recorder chart.

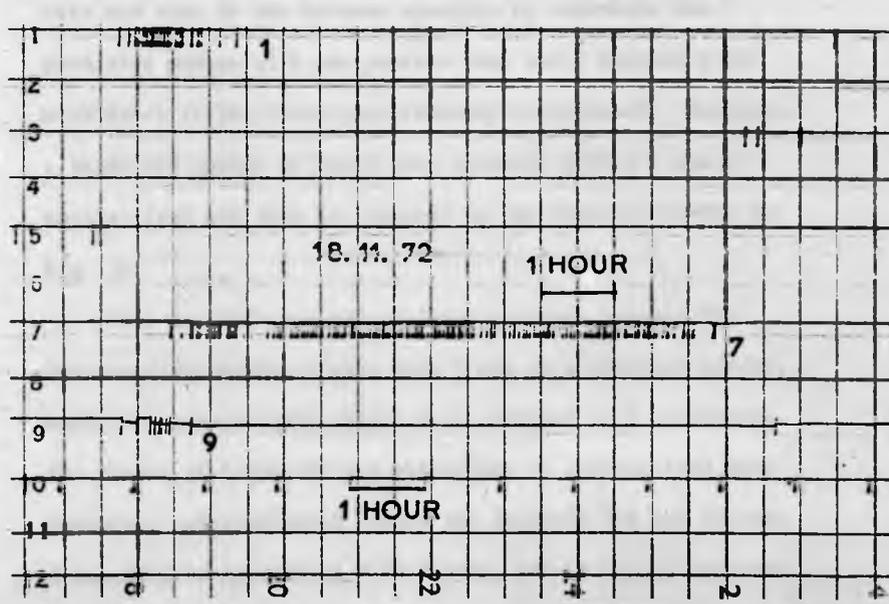
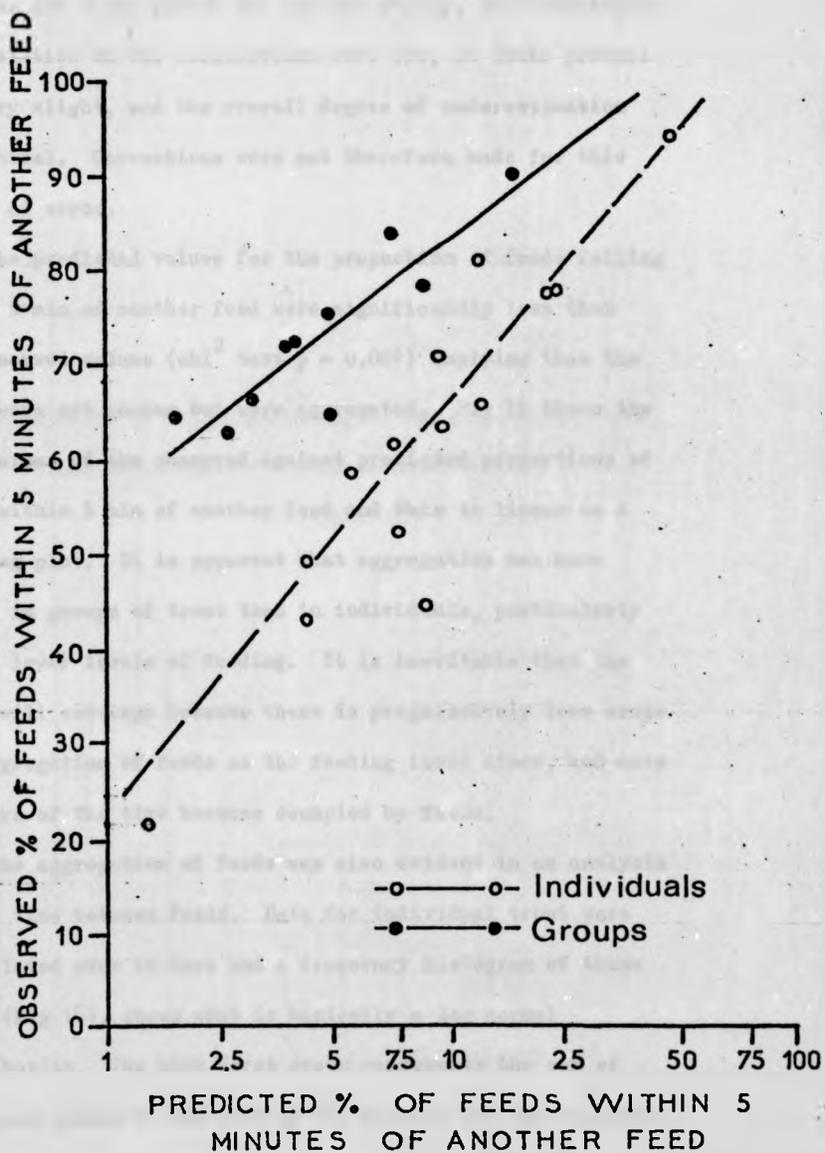


Fig 14. A photocopy of a section of a pen recorder chart showing the way in which feeds are aggregated.

Ten day periods of feeding were analysed for the number of feeds which fell within 5 min of another feed, and this observed proportion was compared to a predicted result based on a Poisson distribution. Because of the high level of overnight feeding observed it was assumed that the trout were potentially able to feed for 24 h a day. The mean number of feeds per 5 min period (m) was calculated and this was used in the Poisson equation to calculate the predicted number of 5 min periods that would contain 2 or more feeds if the feeds were randomly distributed. This gave a predicted number of feeds that occurred within 5 min of another feed and this is compared to the observed number in Fig 15.

This analysis was not strictly complete because the Poisson distribution treats each 5 min as a discrete period, while the pen recorder charts were analysed as a continuum. The number of feeds falling within 5 min of another feed were therefore underestimated, since the analysis did not include 5-min periods containing 1 feed only, but which lay adjacent to 5-min periods containing 2 or more feeds, all feeds being within 5 min of each other. This effect involved the simultaneous occurrence of two unrelated events and the probability of this is calculated by the product of the

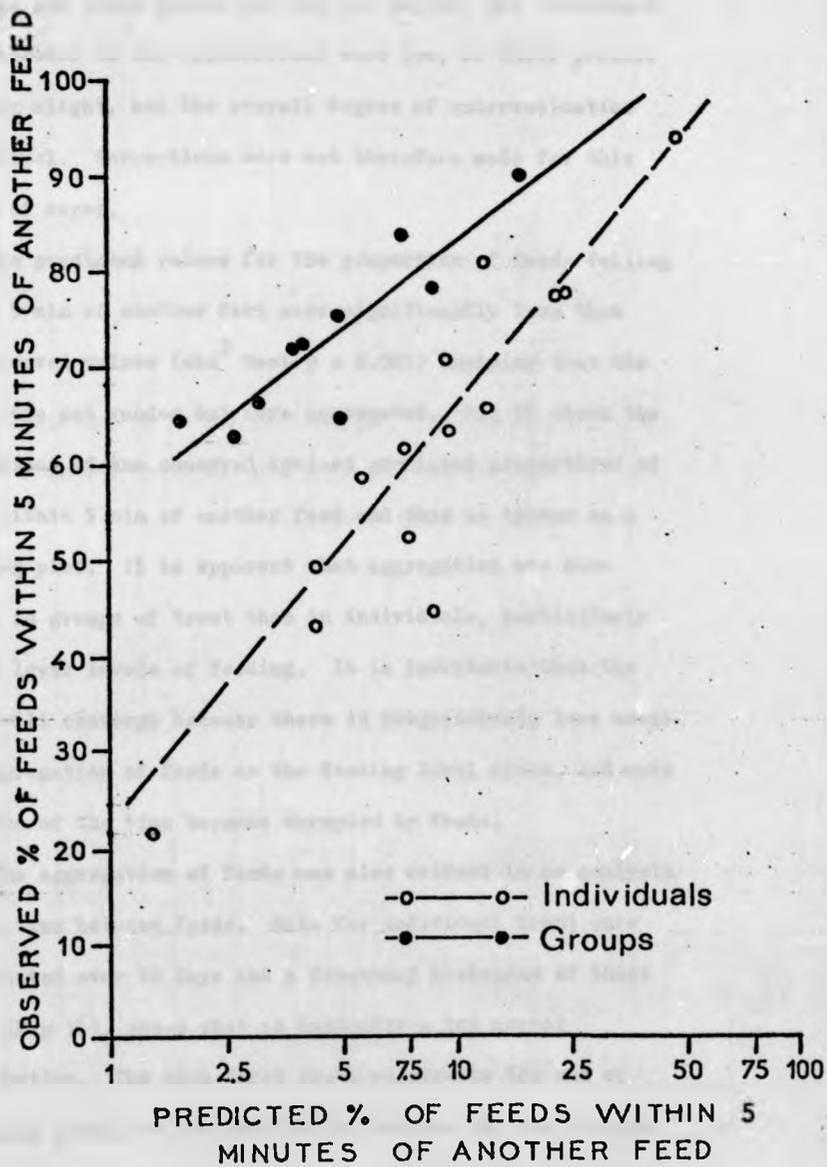
the number
 another feed.
 pected by
 trout.



The first period of feeding was observed for the number of feeds which fell within 5 min of another feed, and this observed frequency was compared to a simulated series based on a Poisson distribution. Because of the high level of overnight feeding observed it was assumed that the time was potentially able to feed for 24 hrs. The number of feeds per 24 hrs was calculated and this was used in the Poisson equation to calculate the expected number of 5 min periods that would contain 2 or

Fig. 15. The aggregation of feeds is evident in the number of feeds that fall within 5 mins of another feed. This is much greater than would be expected by chance, particularly in the groups of trout.

This analysis was not strictly correct because the Poisson distribution applies only to a discrete period, while the observed feeds were not spaced as a continuous series. The number of feeds falling within 5 min of another feed were therefore underestimated, since the analysis did not include 5-min periods containing 2 feeds each, but which lay adjacent to 5-min periods containing 2 or more feeds, all feeds falling within 5 min of each other. This effect involved the simultaneous occurrence of the expected feeds and the probability of this is calculated by the product of the



umber
feed.
by

probabilities of each separate event. Since the mean number of feeds per 5-min period (m) was low anyway, the constituent probabilities in the calculations were low, so their product was very slight, and the overall degree of underestimation was minimal. Corrections were not therefore made for this source of error.

The predicted values for the proportion of feeds falling within 5 min of another feed were significantly less than the observed values (χ^2 test $p = 0.001$) implying that the feeds were not random but were aggregated. Fig 15 shows the regressions of the observed against predicted proportions of feeds within 5 min of another feed and this is linear on a semi log plot. It is apparent that aggregation was more marked in groups of trout than in individuals, particularly at the lower levels of feeding. It is inevitable that the lines will converge because there is progressively less scope for aggregation of feeds as the feeding level rises, and more and more of the time becomes occupied by feeds.

The aggregation of feeds was also evident in an analysis of the time between feeds. Data for individual trout were accumulated over 10 days and a frequency histogram of these data, (Fig 16), shows what is basically a log normal distribution. The high first group represents the sum of histogram groups to the left of it, because the pen recorder

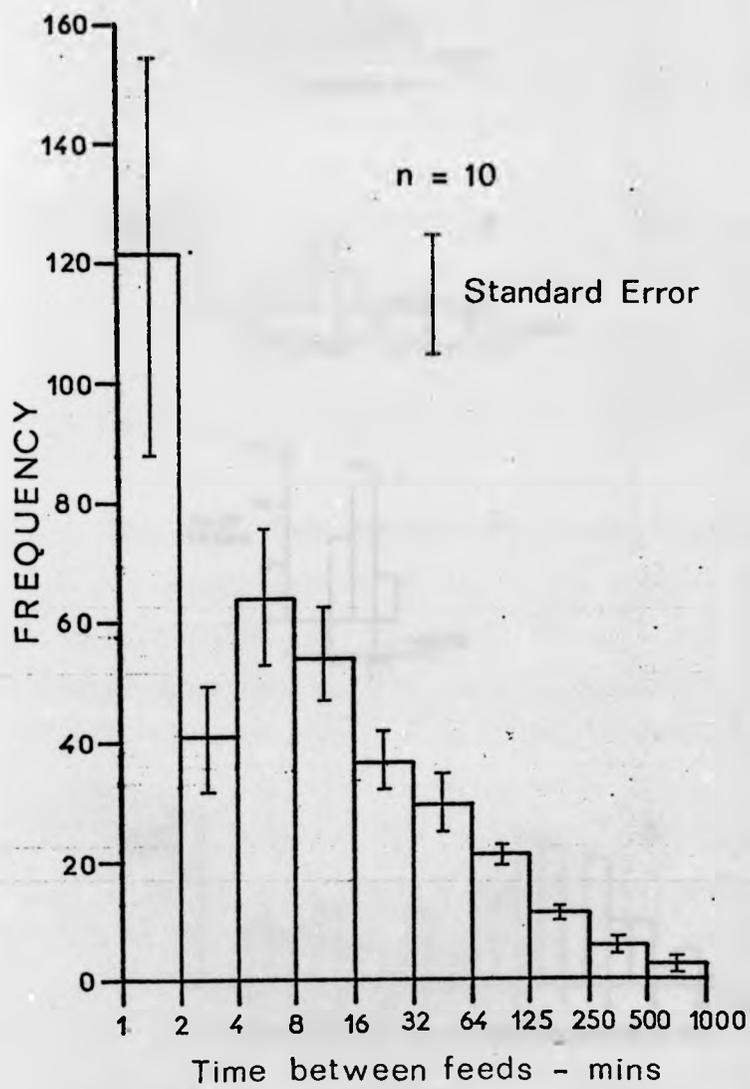
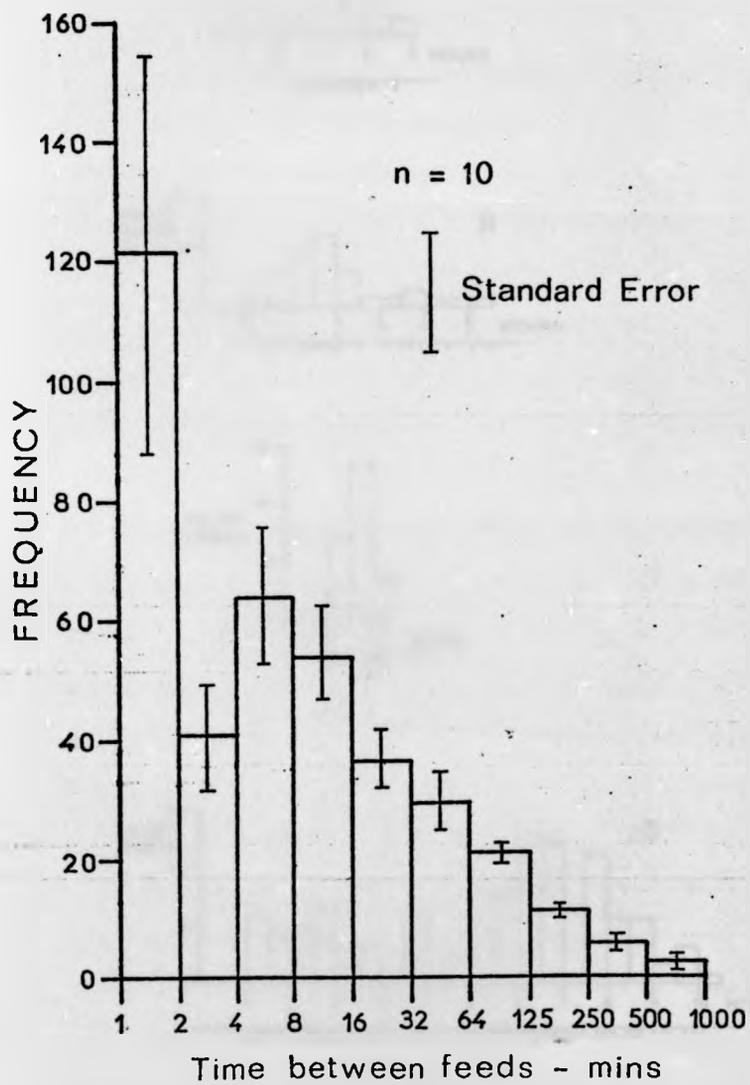


Fig 16. Censored log normal distribution of the time
between feeds showing a preference to feed
at 4 to 8 min intervals.



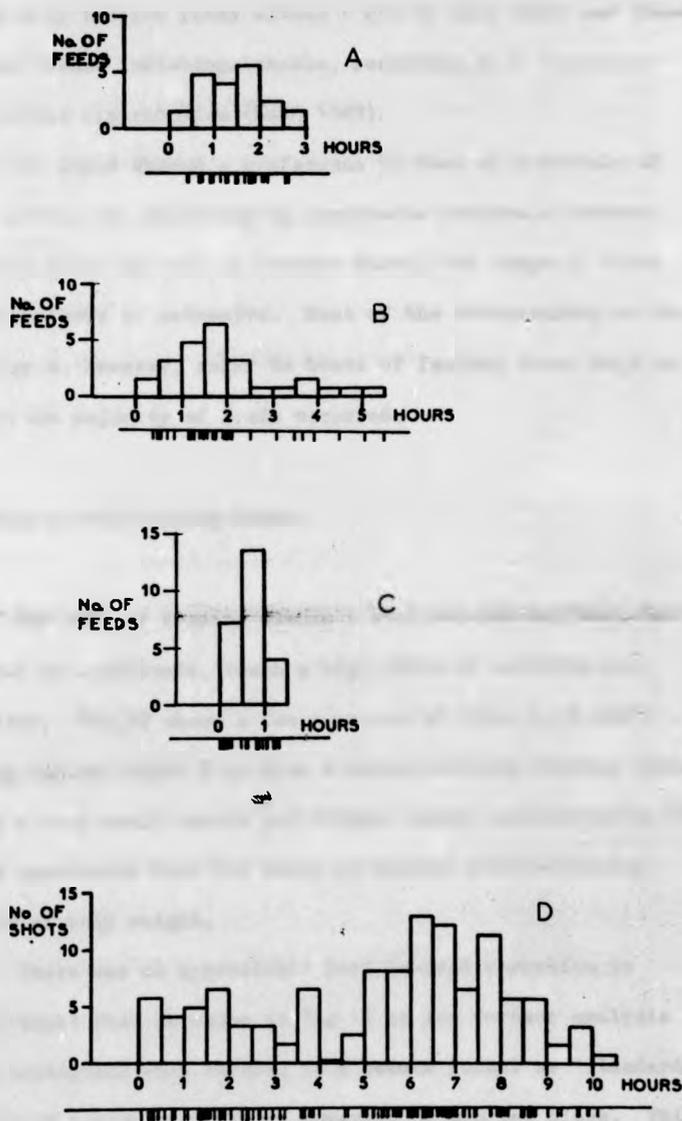


Fig 17. Histograms of patterns of feeding bouts. The pen recorder record is shown below the histograms.

could only resolve feeds within 1 min of each other and these groups become indistinguishable, resulting in a 'censored' log normal distribution (Hald 1949).

The trout showed a preference to feed at intervals of 4 to 8 min, but since Fig 16 represents intervals between feeds ^{within} a bout, as well as between bouts, the range of times between feeds is extensive. Most of the observations in the histogram, however, refer to bouts of feeding since this is where the majority of feeds occurred.

Pattern within feeding bouts.

The rate of feeding within 1 bout was not uniform, but tended to accelerate, reach a high pitch of activity and decline. Fig 17 shows a few examples of this, A, B and C being typical while D is from a large actively feeding trout with a very small reward per trigger press, necessitating in this particular bout 144 shots to deliver food totalling 0.82% of body weight.

There was an appreciable feed-to-feed variation in individual fish as shown in Fig 17 so for further analysis the histograms were reduced to a common format or 'standard feed' of 6 histogram blocks covering 30 min per block. This was done by simple proportionality;

n = number of blocks in the observed histogram of the bouts of feeds.

$n/6$ = Constant C to calculate a standard histogram of bouts of feeds consisting of 6 blocks.

Where t_o = mid time of a block in the observed histogram, and h = the number of feeds in such a block, then this block is represented in the standard histogram by a point at time $t_s = t_o \times 1/C$ and representing a number of feeds given by $h_s = h_o \times C$

The calculated values of h_s and t_s were plotted from a number of histograms referring to the same trout, and a histogram of standard format drawn to fit the calculated data. Such standard feed histograms are presented in Fig 18. The scatter of points is shown for one histogram only, and the final one (which is equivalent to D in Fig 17) is converted to a standard format of 12 blocks, since this was the pattern shown by that particular trout. In this case the pattern of feeding is uniform and intense throughout the feeding bout with some tailing off at the end, but an acceleration and/or deceleration of feeding activity within bouts is observable in the other 5 examples.

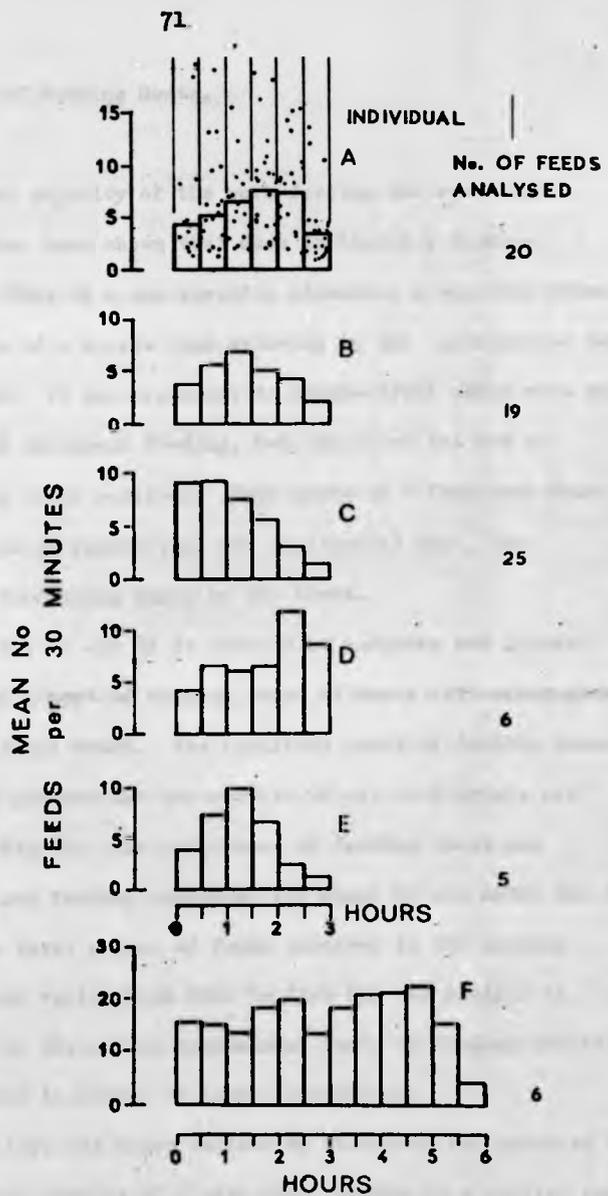


Fig 18. "Standard feed" histograms of the pattern of feeding within feeding bouts.

Initiation of Feeding Bouts.

For the majority of the work feeding was spontaneous, though it has been shown that dusk initiated a feeding response. This is a non specific stimulus; a specific stimulus in the form of a single food delivery by the experimenter was also tested. It was necessary to choose trout which were well established on demand feeding, but which had not fed so recently as to be satiated. Test shots of 1 feed were made at random times on random (but not successive) days, the delivered food being taken by the trout.

Four trials out of 24 induced no response and 20 were followed by a bout of feeding, most of these (17) being done with individual trout. The resulting bouts of feeding showed no obvious pattern and the results of all such trials are pooled in Fig 19. The initiation of feeding bouts was immediate and feeding continued for about 80 min after the test shot. The total number of feeds involved in the ensuing feeding bout varied from fish to fish but was similar in magnitude to the normal spontaneous bouts of feeding exhibited by the trout or groups of trout in question.

This idea was taken further by selecting two pairs of trout in which the members of a pair were feeding at a similar rate. The feeders were then cross connected so that as one of the

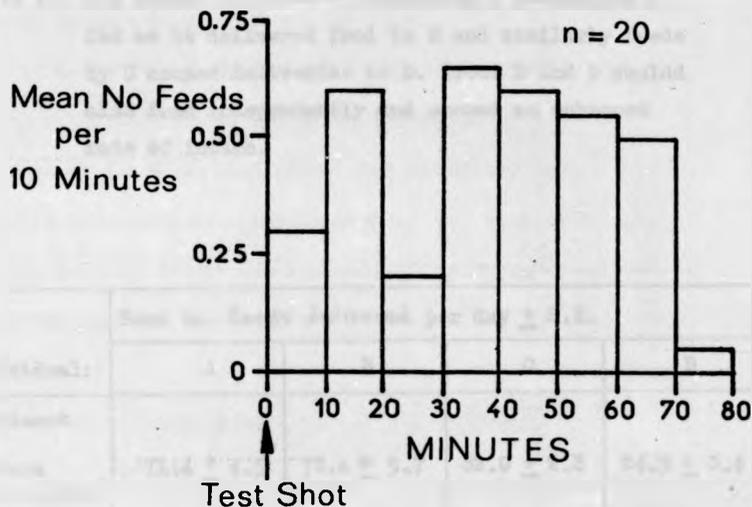


Fig 19. The pattern of feeding in 20 feeding bouts initiated by a single food delivery by the experimenter.

pair, an "operator" fish A, fed, it fired its own feeder as well as that of a subject fish B. Trout B could also feed independently. Similarly a trigger press by trout C fired feeders for C and D, while a trigger press by D fired only feeder D. Table 15 summarises the results.

In each case the subject trout B and D operated the

Table 15. The effect of cross - connecting 2 feeders, as A fed so it delivered food to B and similarly feeds by C caused deliveries to D. Trout B and D could also feed independently and showed an enhanced rate of intake.

Individual:	Mean No. Feeds delivered per day \pm S.E.			
	A	B	C	D
Treatment				
Feeders independent.	73.4 \pm 4.5	73.4 \pm 5.7	32.0 \pm 2.3	24.5 \pm 3.4
Feeders connected.	88.5 \pm 7.6	111.2 \pm 8.4	27.5 \pm 6.6	47.2 \pm 8.4
	Mean intake per day as % of body weight \pm S.E.			
Feeders independent.	2.54 \pm 0.1	3.19 \pm 0.3	1.69 \pm 0.1	0.89 \pm 0.1
Feeders connected.	2.90 \pm 0.2	4.08 \pm 0.4	1.35 \pm 0.3	1.18 \pm 0.2

feeder independently to obtain food over and above that delivered by the action of the operator trout A and C, delivering about 20 extra feeds per day in both cases. The level of food intake was therefore increased in these subject trout when the feeders were cross-connected, although some of

the extra food delivered was wasted, 37% of the increased delivery being wasted by B and 60% by D.

The extra feeds carried out by B and D were for the most part not related to the feeds delivered by A or C; they were at least an hour after such feeds and were generally preceded by a period without any food delivery. This was true of 97% of the independent feeds by B and 96% of the independent feeds by D.

Hierarchy and Territories.

This was considered in terms of observed aggressive behaviour, territoriality, condition factors, and trigger pressing.

Aggressive displays were frequently observed in tanks containing 2 to 8 trout. They consisted of circling behaviour, attacks to the flank and in extreme cases mouth to mouth attacks and contact. Displays were particularly vigorous between newly introduced trout for the first 24 h. Aggression was serious enough in small (56 and 144 l) tanks to make it difficult to maintain small groups of up to 8 fish, there being a progressive mortality of trout lower in the hierarchy. Table 16 gives an example.

This decline was overcome by putting net barriers of 1 cm

Table 16. Progressive mortality among the smaller members of a group of 8 rainbow trout.

Date.	3.11.72	5.12.72	4.1.73	31.1.73	19.2.73
Ranked weights. grams.	105	108	120	136	149
	100	105	113	130	149
	95	104	82	91	100
	94	93	dead	dead	dead
	68	74	76	65	dead
	59	dead	dead	dead	dead
	52	dead	dead	dead	dead

wire mesh into tanks to reduce interaction between trout. This resulted in a definable territoriality which was quantified by cold branding each trout in a tank of 5 fish and noting the positions of the trout on a total of 51 occasions, observations being made through a hole in a paper

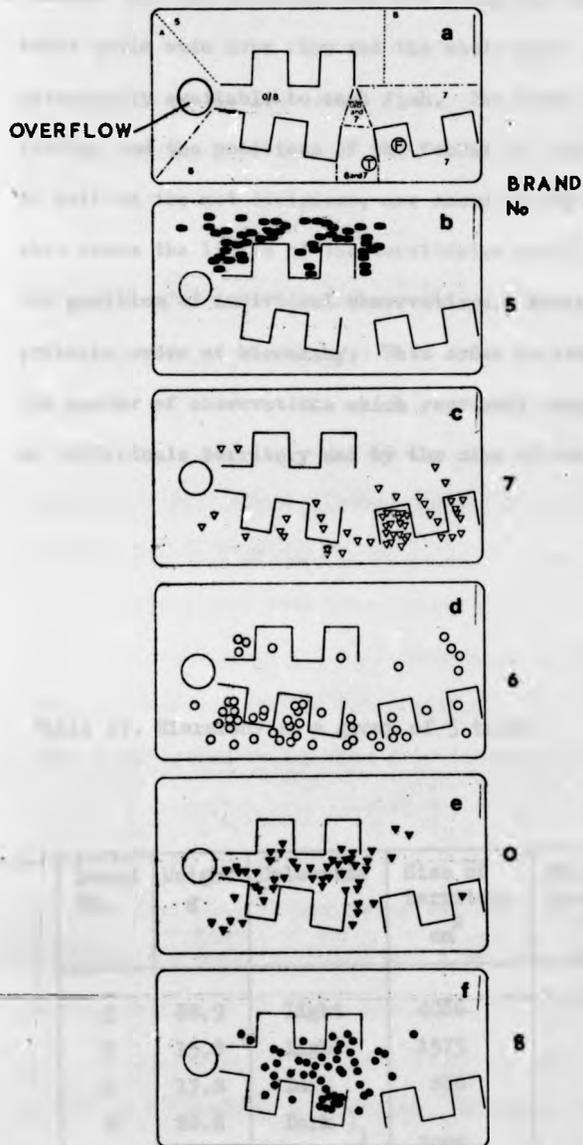


Fig 20. Territories shown by each member of a group of 5 trout in a rectangular tank. The positions of the feeder and trigger are denoted by F and T.

screen. The net divisions did not reach the surface so trout could swim over them and the whole tank was potentially available to each fish. The trout were demand feeding and the positions of the feeder (F) and trigger (T) as well as the net divisions, are shown in Fig 20 a. This also shows the limits of the territories and 20 b-f indicate the position of individual observations. Table 17 gives the probable order of hierarchy. This order is determined by the number of observations which represent incursions into an individuals territory and by the size of the territories.

Table 17. Hierarchy in a group of 5 trout.

Brand No.	Weight g	Colouring	Size of territory cm^2	No. of incursions into territory by other fish.
5	38.9	Light	4036	9
7	15.3	Light	1575	11
6	17.8	Dark	863	14
8	23.6	Dark)	1002	10
0	20.6	Dark)		

Trout number 5 not only occupied the largest territory, but resisted invasion at the extreme periphery of the territory. By contrast the territories of the other 4 fish overlapped and trout 0 and 8 co-habited the same area. Light sandy coloured fish were apparently less stressed than dark ones.

Although it was the largest trout which was number 1 in the hierarchy, it was the smallest which was number 2. The trout were all rather small to be in sea water and it could be that the success or otherwise of acclimation left some fish in a better state to establish a strong hierarchichial position before others.

Territorial effects were investigated in a large round tank (180 cm diameter, 1145 l) containing 21 rainbow trout. This tank was not divided by partitions. Photographs were taken looking vertically down into the tank by a cine camera operating overnight on a time clock, so there was no disturbance of the trout. Normal room lighting was used for illumination. The distance between each fish and its nearest neighbour was measured from these films, and this was used in the analysis of Clarke and Evans (1954) which gives probability levels for individuals being aggregated, dispersed or randomly distributed. A random distribution was consistently indicated for situations with no feeder in

in the tank, with a feeder and trigger present and adjacent, and with the feeder and trigger separated. No evidence of territoriality either with, or without reference to the feeder was therefore observed.

Hierarchy and Trigger Pressing.

Out of 63 feeds recorded with the group of 5 trout previously described, 62 trigger presses were by fish number 5 and 1 by number 7. In spite of being dominant number 5 did not choose a territory which included the feeder, but rather ignored all territorial boundaries while feeding. It could be repeatedly observed to swim over the net divisions and operate the feeder, returning in due course to its own territory.

Several other groups of trout were branded and either photographed or observed directly during feeding, with the results summarised in Table 18.

Although the feeding trout in a group was consistently well up the size range, it was not necessarily the largest. All feeding bouts were initiated by the dominant trout but at the height of a feeding bout the trout were often observed to be very excited and swam continually near the trigger or point of food delivery. At such times a non-dominant fish

Table 18. The results of hierarchy effects in 4 groups of trout. In each case a single individual was dominant as regards trigger pressing. This individual was not necessarily the largest.

No. of fish in group	No. of feeds observed	No. by one individual	Rank wt of feeding fish	Wt. as % of largest fish	Sex
2	58	57	Largest	100%	♂
4	15	15	Largest	100%	♂
11	25	20	3rd Largest	82%	♀
20	50	50	4th Largest	69%	♂

may press the trigger, but this was not common. This excitement effect was more marked in larger groups.

Although the trigger presses were predominantly by one individual, all members of a group took the food delivered.

There was correlation between condition factor (weight/

/length³) and the ranked weights of members of a group, but condition factor was lower in smaller trout anyway (Fig 21) and when this effect was removed there was no discernable reduction in condition factor with a lower rank weight. There was no evidence, therefore, that the trout lower in the hierarchy were deprived of food to the point of losing condition. The points for Fig 21 are all from individual trout or from means only of groups of trout.

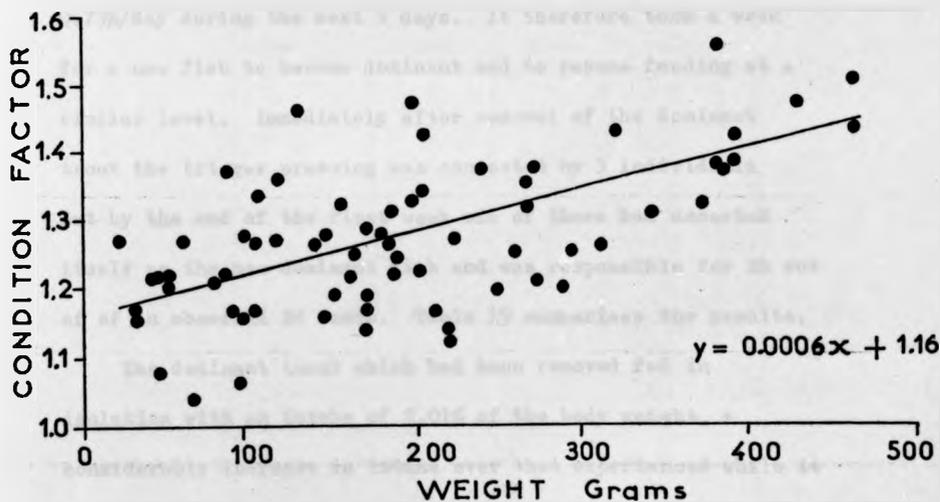


Fig 21. The relationship between the condition factor and size.

In a group of 3 trout removal of the largest individual which did all the trigger pressing caused a virtual cessation of feeding from a previous average intake of 3.78% per day of the body weight of the fish, (averaged over 12 days). The trout that had been removed demand fed in isolation with an intake of 1.85% day of the body weight (averaged over 7 days). Removal of the feeding trout from a group of 11 fish was preceded by an intake of 0.66 %/day of the total weight of fish present (averaged over 12 days) and followed by an intake of 0.07%/day averaged over 7 days. This increased to 0.73%/day during the next 5 days. It therefore took a week for a new fish to become dominant and to resume feeding at a similar level. Immediately after removal of the dominant trout the trigger pressing was contested by 3 individuals but by the end of the first week one of these had asserted itself as the new dominant fish and was responsible for 26 out of of an observed 34 feeds. Table 19 summarises the results.

The dominant trout which had been removed fed in isolation with an intake of 2.01% of the body weight, a considerable increase in intake over that experienced while it was in a group. The reward per trigger press was similar in both situations but the trout in isolation had ample time to consume all the food delivered since it was not taken by other individuals.

Table 19. Three trout in a tank of 10 fish operated the demand feeder after the dominant fish was removed, after 1 week, however, trout number 0 became dominant.

Brand No.	8	7	0
Days	Feeds	Feeds	Feeds
1	1	0	0
2	1	0	2
3	0	0	0
4	0	4	3
5	1	0	4
6	0	0	0
7	0	0	2
8	0	1	15

Further experiments were made with a group of 21 trout, of mean weight 142 g in which the feeder was placed centrally

in a large 180 cm diameter tank with 1 trigger 50 cm from it. The reward level was low, 0.008% of the total fish weight per trigger press. After 17 days this was increased to 0.070% and after a further 9 days two more triggers were added, both 50 cm from the feeder and all widely separated. Table 20 summarises the procedure and results.

Table 20. The effect of adding additional triggers and changing reward levels in a tank of 21 trout.

Treatment:	Intake as % body wt \pm S.E.	No.days
1 trigger, small reward.	0.190 \pm 0.046	17
1 trigger, large reward.	0.615 \pm 0.176	9
3 triggers, large reward.	0.761 \pm 0.024	32
Hand Fed.	0.795 \pm 0.024	7

N.B. Small reward 0.008% of total fish weight.

Large reward 0.070% of total fish weight.

The increase in reward level with only 1 trigger present caused a considerable increase in intake, and the addition of two extra triggers caused a further small increase in food intake. There was no wastage at any time. The actual number of trigger presses was in fact very low, with a mean of 12.31 presses per day with three triggers present. Each trigger operated through a separate relay and counter and this 12.3 presses per day was made up as shown below.

Trigger No.	Mean No. presses/day.	S.E.
1	1.4	0.38
2	6.5	1.05
3	4.4	0.82
Total.	12.3	

These means are all significantly different ($p = 0.001$) and a preference for trigger number 2 was evident. This was the original trigger in the tank before the other two were added.

The trout were cold-branded and each trigger filmed in turn to see which trout used which trigger. This was not successful because the room lighting was inadequate and definition was very poor. The addition of an extra light over the tank disrupted the feeding pattern. The distribution

of feeds after adding the light being :

Trigger.	Mean.	No. days.
1	1.0	10
2	2.5	10
3	5.7	10

Attempts to use a flashgun caused a lot of disturbance of the trout.

Growth, Intake and Food Conversion Efficiency.

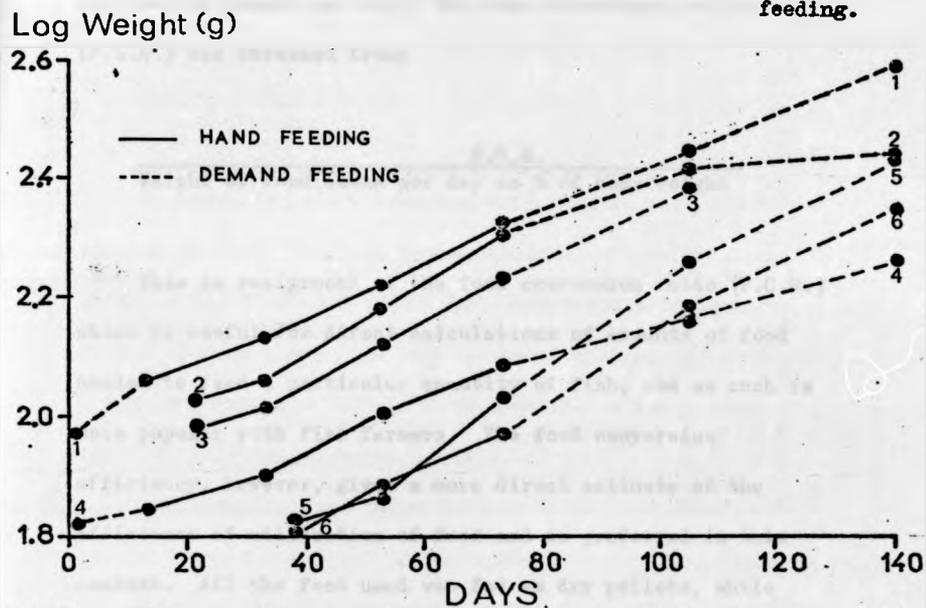
Individual Trout.

The growth of individual trout at 11°C is shown in Fig 22 and the accompanying table summarises the growth data for these fish. The specific growth rate (S.G.R.) was calculated from the equation given by Brown (1957)

$$SGR = \frac{\log_e Y_T - \log_e Y_t}{T - t} \times 100$$

Where Y_t and Y_T are the initial and final weight in grams at times T and t. Time was measured in days. This gives %

Fig 22. Growth data for 6 individual trout on hand and demand feeding.



FISH No	1	2	3	4	5	6
1	SGR 1.82	1.06	1.24	1.32	1.08	1.15
	FCE 0.82	0.48	0.45	0.46	0.72	0.93
2	SGR	0.49	1.99	1.99	0.86	
	FCE	0.35	0.77	0.71	0.31	
3	SGR	0.63	1.64	1.63	1.20	
	FCE	0.27	0.39	0.53	0.26	
4	SGR 0.52	0.84	1.27	1.18	0.67	0.60
	FCE 0.25	0.32	0.40	0.35	0.26	0.17
5	SGR		0.74	2.08	1.68	1.21
	FCE		0.48	0.49	0.53	0.46
6	SGR		1.12	1.23	1.45	1.45
	FCE		0.44	0.56	0.30	0.55

increase in weight per day. The food conversion efficiency (F.C.E.) was obtained from;

$$\frac{\text{S.G.R.}}{\text{Weight of food eaten per day as \% of body weight}}$$

This is reciprocal of the food conversion ratio (F.C.R.) which is useful for direct calculations of amounts of food needed to feed a particular quantity of fish, and as such is more popular with fish farmers. The food conversion efficiency, however, gives a more direct estimate of the efficiency of utilisation of food and is preferred in this context. All the food used was fed as dry pellets, while the fish were weighed live, as wet weight, so it was possible to get a F.C.R. of 1.0 or more.

The effect of a changeover from feeding to satiation by hand twice a day to demand feeding was variable and was accompanied by either an increase in food conversion efficiency (more efficient utilisation of food) e.g. fish numbers 1 and 5, or a decrease e.g. fish numbers 2, 3, 4 and 6. The means of the data in Fig 19 showed no significant differences between hand and demand feeding;

Hand feeding. Periods 2, 3 and 4. n = 16.

S.G.R. mean = 1.278 S.E. = 0.121 %/day

F.C.E. mean = 0.467 S.E. = 0.033

Demand feeding. Periods 1, 5 and 6. n = 12.

S.G.R. mean = 1.043 S.E. = 0.122 %/day

F.C.E. mean = 0.461 S.E. = 0.072

Growth rates and conversion efficiencies were therefore similar for both hand and demand feeding. No correlation could be found between intake and conversion efficiency in either hand or demand fed trout, the conversion efficiencies being very variable both between individuals and within individuals between growth periods.

A correlation was found between daily food intake and reward level per trigger press as shown in Fig 25. The mean voluntary levels of food intake varied from 1.9% of the body weight per day at a reward level of 0.02% of the body weight per trigger press, (i.e. a total of 98 trigger presses per day) to an intake of 3.1% of the body weight per day with a reward level of 0.11% of the body weight, a total of 28 trigger presses per day. These figures are exclusive of wasted food. This compares with a mean intake of 2.74% of body weight (S.E. 0.20%) when hand fed twice a day to satiation. The change of intake with different reward levels was investigated over a wider range of rewards with 40 further individuals and these data are presented in Fig 26 in comparison with similar data for groups of trout.

Daily intake %
of body weight

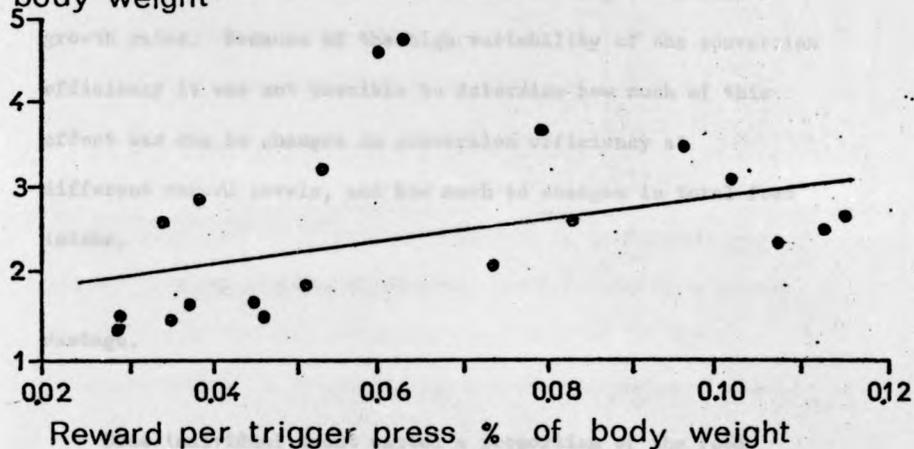


Fig 23. Relationship between reward per trigger press and intake.

SGR %/Day

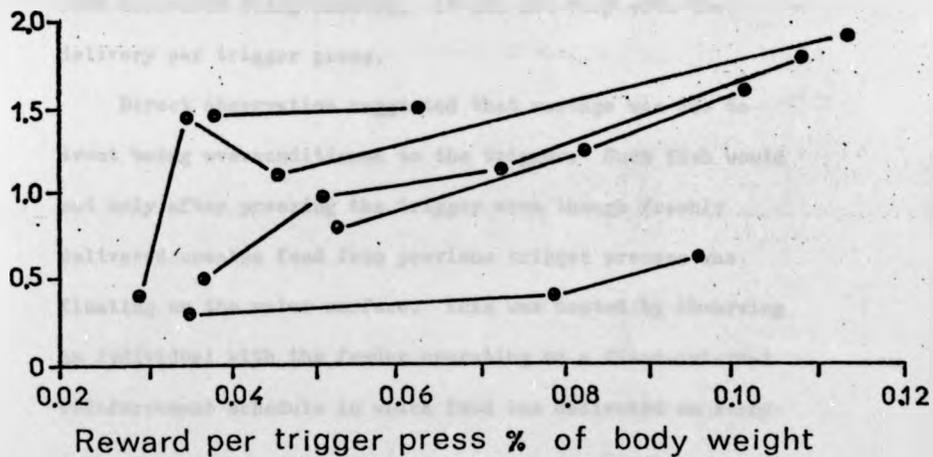


Fig 24. The effect of changing the reward on the growth of 5 individual trout.

The reward level affected the growth rate of individual trout (Fig 24), increased reward levels leading to increased growth rates. Because of the high variability of the conversion efficiency it was not possible to determine how much of this effect was due to changes in conversion efficiency at different reward levels, and how much to changes in total food intake.

Wastage.

Some individual trout wasted a proportion of the food delivered, while some did not. This was constant within an individual so trout could be classified as wasters or non-wasters, the wasters being more common. The wastage levels were relatively uniform with a mean of 24% (S.E. 2%) of the food delivered being uneaten. It did not vary with the delivery per trigger press.

Direct observation suggested that wastage was due to trout being overconditioned to the trigger. Such fish would eat only after pressing the trigger even though freshly delivered uneaten food from previous trigger presses was floating on the water surface. This was tested by observing an individual with the feeder operating on a fixed-interval reinforcement schedule in which food was delivered on every

5th trigger press. The trout was repeatedly observed to operate the trigger on a non-reinforced feed and proceed to eat a pellet left over from a previous delivery. The mean delivery per trigger press was 2.98 pellets (S.D. 1.26). Table 21 compares intake and wastage when 1:1 and 1:5 schedules of reinforcement were alternated. From the overall means a very significant difference was observed in both intake and wastage between the two schedules. The 1:5 reinforcement had the effect of reducing intake to about half of the level observed with a 1:1 schedule, and wastage was reduced to about one third of the previous level.

On a 1:1 schedule the trout recorded as many as 375 trigger presses per day, the mean being 152 (S.E. 19.7). On the 1:5 schedule the mean number of trigger presses per day was 205 (S.E. 18.5) of which only one in 5 was rewarded. There was therefore a small increase in trigger pressing effort to counteract the reduction in reward levels, but certainly not a 5 times increase which would negate the effect of a 1:5 schedule.

Groups of Trout.

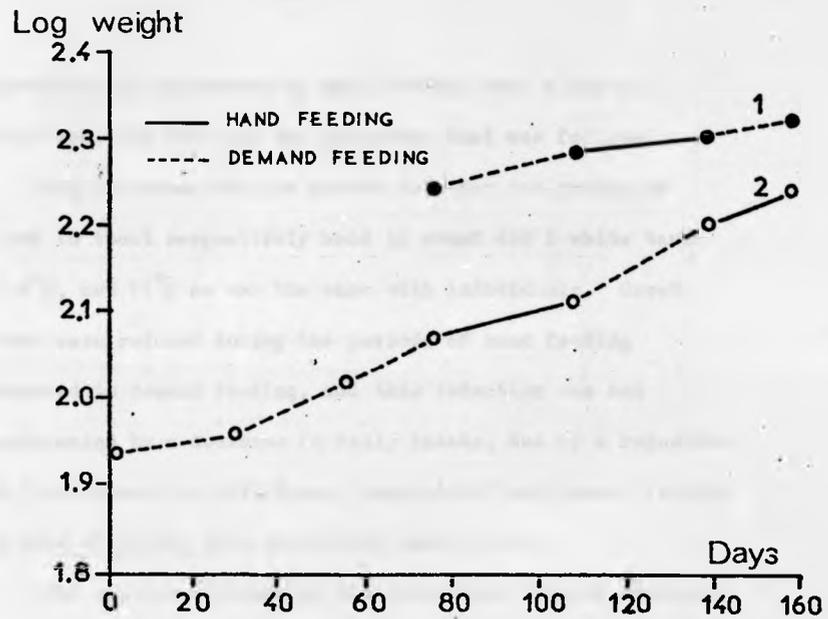
Small groups of trout were difficult to establish and maintain for long periods because of strong hierarchy effects. Growth results are therefore confined to two groups of trout

Table 21. The effect of a 1:1 and a 1:5 fixed interval reinforcement ratio on intake and wastage in an individual trout.

Reinforcement Schedule.	Mean intake % of body wt.	Mean waste % of total delivery.	No. days
1:1	3.30	47	7
1:5	1.75	26	15
1:1	3.83	28	4
1:5	1.25	0	15
1:1	2.82	30	7
Overall:	+ S.E.	+ S.E.	
1:1	3.32 ± 0.47	41.2 ± 4.0	18
1:5	1.49 ± 0.53	13.0 ± 4.2	30

for comparison between hand and demand feeding.

With individuals the food intake when fed twice a day to satiation was comparable to the daily intake on demand feeding. In groups of trout, however, the daily intake with demand feeding was less and could be



TANK							
2							
Intake	1.52 %	1.12 %	1.29%	1.25%	1.24 %	1.17 %	
SGR	0.19	0.47	0.59	0.46	0.52	0.42	
FCE	0.12	0.42	0.45	0.36	0.42	0.36	
1							
Intake				0.68%	0.79%	0.69%	
SGR				0.29	0.19	0.29	
FCE				0.43	0.25	0.42	

Fig 25. Growth of two groups, ^{one} of 10 (tank 1) and ^{one of} 7 (tank 2) rainbow trout with hand and demand feeding

approximately reproduced by hand feeding once a day to satiation, and this was the procedure that was followed.

Fig 25 summarises the growth data for two groups of 7 and 10 trout respectively held in round 430 l white tanks at 8°C, not 11°C as was the case with individuals. Growth rates were reduced during the periods of hand feeding compared to demand feeding, and this reduction was not accompanied by a decrease in daily intake, but by a reduction in food conversion efficiency, suggesting that demand feeding is more efficient than once-daily hand feeding.

The results of changing the reward per trigger press are shown in Fig 27, and the results similarly obtained from individuals are shown in Fig 26. In all cases the points represent means of observations of 15 to 30 day periods. In the case of both groups and individuals the level of intake rises rapidly with the level of reward and reaches a plateau after reward levels of 0.1% of the body weight. For individuals this is 0.1% of the weight of 1 fish, whereas for groups it is 0.1% of the total weight of trout in the group. In purely mechanical terms, therefore, deliveries per trigger press to groups need to be greater than to individuals, in a proportion to the number of trout in the group. The actual number of trigger presses per day decreases in response to increased reward levels (dashed lines) in both individuals

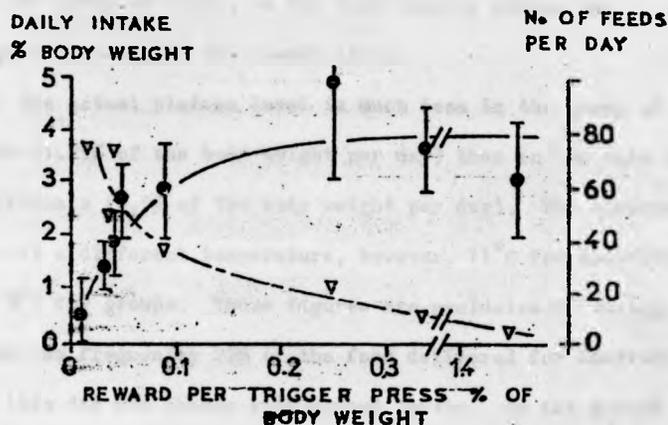


Fig 26. Relationship between intake and reward levels for 4 individual rainbow trout. The closed circles represent the mean intake during 25 days observation on 1 trout with the 95 % confidence limits, thus each trout was used at 2 reward levels. The triangles show the number of trigger presses.

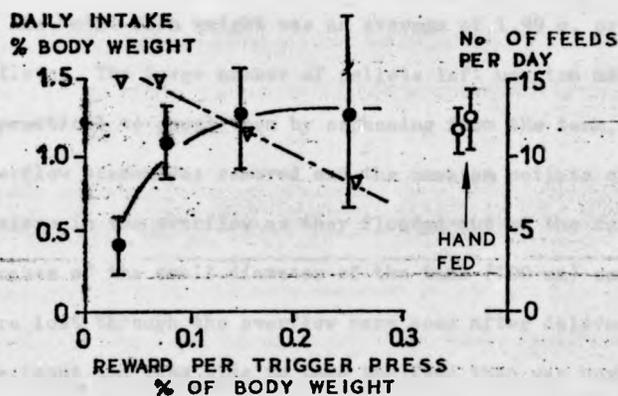


Fig 27. The effect of varying the reward level with a group of 7 trout of about 100 g. Closed circles: mean of 25 days observation with 95 % confidence levels, triangles: number of trigger presses.

and the group of trout, so the fish clearly relate the trigger pressing to the reward level.

The actual plateau level is much less in the group of trout (1.25% of the body weight per day) than in the case of individuals (3.5% of the body weight per day). The experiments were at a different temperature, however, 11°C for individuals and 8°C for groups. These figures are exclusive of wastage which was frequently 25% of the food delivered for individuals, and this did not change with reward levels. In the groups of trout there was no wastage at low reward levels, food only being wasted at a reward level of 0.256% of the total fish weight per trigger press, at which level it was considerable, with a mean of 75.16% of the food delivered being uneaten. This high level of wastage is due in part to the experimental arrangement. The actual delivery per trigger press at 0.256% of the total fish weight was an average of 1.99 g, or 185 pellets. The large number of pellets left uneaten made it impractical to count them by siphoning from the tank, so the overflow screen was removed and the uneaten pellets caught by a sieve in the overflow as they floated out of the tank. Because of the small diameter of the tank (100 cm) some pellets were lost through the overflow very soon after delivery and the trout had less time to take the food than was normally the case.

Variations in reward level over a less extensive range were made with another group of 15 trout of mean weight 152 g. The reward level was raised from 0.015 to 0.028% of the total fish weight resulting in a change of intake from 0.504 (S.E. 0.034) to 0.919 (S.E. 0.105) % of the fish weight. There was no wastage at either reward level. The food manufacturers recommended feeding level for trout of the size involved at 8°C was 0.7% of the fish weight, so it was possible to manipulate the intake around this by changing reward levels.

Trout Growth in the Sea Cages.

Because of the problems of maintaining equipment on the sea cages demand feeding was restricted to short runs to train trout, as reported earlier on page 45. For most of the time the sea cages were principally a means of acclimating and maintaining stocks of fish, and trout were only fed every second day when fully acclimated.

One group of 64 trout was fed daily to satiation for a short period to obtain an assessment of the growth rate which could be expected in cages. The water temperature was 14°C, 15°C being the highest temperature obtained for any length of time in Dunstaffnage Bay. Table 22 shows the results.

Table 22. Comparison between feeding daily and every 2 days on growth and conversion by rainbow trout in a sea cage.

Treatment.	Growth.	SGR	Intake % wt per day	FCE	No. Days.
Fed daily	32.9 to 42.6g	1.72	2.12	0.81	15
Fed every 2 days.	42.6 to 54.6g	0.60	1.60	0.40	40

The daily intake when the trout were fed to satiation every 2 days is not simply half that obtained when they were fed to satiation once daily. As would be expected they compensate by taking more food before being satiated on the 2-day feeding schedule. There is, however, a reduction in specific growth rate of more than a 1:2 ratio and this is due largely to the much reduced conversion efficiency on the 2-day feeding regime.

The daily intake of 2.1% of the fish weight on a once daily feeding schedule was the same as the feeding level recommended by the food manufacturers for 20 to 30 g trout

at 14°C, although they recommend that this be distributed over 3 or 4 feeds per day.

Two cages of 53 trout were hand-fed daily during a winter period to assess growth in cold water. The growth rates recorded over a 40 day period from December to January at a temperature of 8°C are summarised below.

Cage.	Growth.		Intake % day.	S.G.R.	F.C.E.
	From	To			
1.	162.0	188.4 g.	0.94.	0.370.	0.392.
2.	166.3	193.1 g.	0.98.	0.374.	0.378.

There is close agreement between the two cages.

Two further sea cages each containing 58 trout of mean weight 279 g were established in the summer and one cage hand-fed once a day to satiation, the other being on demand feeding. The demand feeding trout fed actively, recording an average of 138 feeds per day over a 12 day period. The reward level was 0.022% of the total fish weight, so the mean daily intake was 2.99% of the fish weight. As with laboratory experiments this was a similar intake to the once daily hand-fed trout which consumed 2.47% of the body weight per day.

The water temperature was 14.5°C at which temperature the manufacturers levels of feeding are 1.1% per day. These

trout were, however, at market size and at this size the manufacturers recommendations are aimed at optimising conversion efficiency rather than growth rate, hence the lower feeding rate suggested.

No assessment was made of food wastage in sea cages so conversion efficiency figures derived from cage experiments are inclusive of wastage. Wastage was minimised when hand feeding by controlling the rate at which food was added and in the case of demand feeding food was delivered in small amounts at intervals so wastage would not be expected to be very great.

DISCUSSION

Acclimation to Sea Water.

The adaptation of salmonids to sea water is the subject of an extensive literature, summarised by Parry (1966) and Kinne (1964). Trout in sea water drink large volumes, Parry (1966) reports 4-6% of the body weight per hour, and Conte (1969) gives a figure of 0.3 to 1.5% per hour. A considerable metabolic load is incurred in removing the excess salt via salt secreting glands in the gills (Parry, Holliday and Blaxter 1959, Rao 1971) where the main osmotic control is

exercised, although there is a lesser amount of renal and intestinal exchange (Holmes and Stainer 1966, Shehadah and Gordon 1969).

Rates of exchange of ions on initial acclimation of seawater show an initial adjustive phase of about 7 days when plasma levels of Cl, Na and K are elevated, followed by a return to normal levels (Houston 1959, Gordon 1959, Gordon 1963, Parry 1960). This correlates with my findings of maximum mortality within the first 10 days after acclimation. The ability of a trout to survive these changes depends on fish size (Conte and Wagner 1965) and water temperature (Gordon 1959) lower water temperatures favouring acclimation.

Conte and Wagner (1965) give a detailed table of rainbow trout sizes correlated with survival after acclimation to sea water at 30% at different times of the year. High survival levels were obtained in Nov/Dec and April for trout of 35 to 65 g. In a later paper Conte (1969) gives more details of different species and at salinities from 20 to 30%. Although his information is not complete for Salmo gairdneri, survival of fry (3-4 cms) is good at 20% though it is reduced at increasing salinities.

The initial difficulties experienced in the laboratory in acclimating trout can be traced to the difficulty of

maintaining recirculating systems on an adequate scale to hold large numbers of trout and to the strong hierarchical effects in holding small numbers of fish leading to an additional non-osmotic stress. The success of the sea cages was due to the larger scale of operation and the excellent water quality, with a total water interchange in as little as 1 min with a strong tide. The reduced salinity during periods of high rainfall was also highly advantageous, particularly since there was minimal stratification of water within the cages, the hydrography of the area causing adequate mixing. The only group of trout acclimated in the sea cage at a high salinity averaged 115 g in weight and were apparently large enough to acclimate easily.

It is the opinion of trout farmers using sea water (Harden pers. comm.) that acclimation becomes difficult only above 27‰ and my results support this, mortality in the recirculating systems only occurred with salinity changes over 25‰. There is no obvious reason why 27‰ should be a critical level. Rao (1971) studied oxygen consumption in rainbow trout at various salinities and found a minimal oxygen consumption at 7.5‰ (isotonic) with a steady increase with salinity above this level. There was, however, no point of inflection in the relation between oxygen consumption and salinity at 27‰.

The use of wet food, either minced squid or pellets soaked with fresh water, during acclimation would reduce the need to drink sea water and so reduce the osmotic load. The pellets absorbed about their own weight of water, 10 g of Coopers size 4 pellets absorbing 12.27 g of water and 10 g of size 5 absorbing 9.34 g of water. At a feeding level of 4% of the body weight per day the soaked pellets only provide 4% of the body weight of water per day. According to the figures of Parry (1966) this is only equivalent to 1 h drinking, so the effect is not great. Since it is the increase in salinity from 27‰ upwards, however, which is responsible for much of the stress, it is possible that this relatively small advantage in water intake is adequate to help offset the stress effects due to the increase of salinity above 27‰. Some food firms are thinking of a very hygroscopic pellet which will absorb much more water (de Ruijter, pers. comm.).

Stocking densities in the sea cages were not high being 1.86 Kg/m³ for the smallest trout used (mean weight 31 g) and 6.90 Kg/m³ for the larger 115 g trout. This compares to a commercial density of 20 Kg/m³ (Shorthouse pers. comm.). The trout were therefore minimally stressed by density effects. Mukai (1973) acclimated 60 g rainbow trout to 30‰ over a 10 day period of increasing salinity with a generous flow of

water at a controlled salinity. He recorded a 99.5% survival at stocking densities of 7.2 and 14.4 Kg/m³ feeding dry food throughout.

Since stress effects are cumulative the prudent trout farmer using sea water would minimise stress from any source during the adjustive phase. This means keeping stocking densities low, feeding wet food and avoiding all fish handling.

Pelleted Food.

The dry food used for all experimental work was a product of Coopers Nutrition Ltd. It was in the lower range of food prices, the cost being directly proportional to the protein level, which in turn effects the conversion efficiency. Digestibility of protein, particularly animal protein, is in the order of 90% in trout (Phillips 1969) so that most of the food will be absorbed. There is an upper limit to the protein level in the food since an excess will be deaminated and used as a source of energy rather than for tissue growth and repair (Covey and Sargent 1972) although this is an economic rather than a biological restraint.

Floating food was used in tanks, but sinking food was more satisfactory for the cages, where there was a greater depth of water available for the trout to take the food. Any

waste was lost through the cage bottom. Sinking food helps to overcome hierarchy effects since it is distributed more evenly over the volume of water available to the trout.

Learning.

Individual trained trout learned to feed and reached a plateau level within 7 days, as did untrained individuals, though these fed less well for the initial 7 days. Groups of trout learned to operate the trigger and reached a plateau level in 2 days without training. Welty (1934) showed goldfish learnt to run a maze more quickly in groups than as individuals, and Adron et al (1973) using rainbow trout in freshwater with a mechanical trigger reported a 10 day period before untrained groups of 30 trout reached a plateau level of feeding. These trout recorded more feeds per day than those described in Table 11, so that the difference in learning rate is not due to a difference in the number of "trials" that the trout experienced per day. At 14-16 g the trout Adron used were smaller than those described in Table 11. Adron et al also report that trained trout learnt to nudge the trigger gently rather than attack it with unnecessary force. This corresponds in general to my own observations for smaller trout, but cine records of

experienced larger fish (150 to 200 g) show violent trigger pressing activity particularly at the height of feeding bouts.

The cine records also demonstrate that the trout learnt to economise in their swimming activity in that they operated the trigger from an angle which allowed them to swim to the point of food delivery with the minimum of effort. This was particularly apparent with the light-operated trigger where small trout would glide through it on route to the feeder, and large trout would insert their head into it, withdraw it and swim to the food with one very economical movement. Adron *et al* (1973) made similar observations.

The enhanced rate of learning in groups is evidence of social facilitation. Since one individual becomes dominant in the trigger pressing, however, trigger pressing by other trout must be repressed, a social repression. The two effects are opposed. The apparent anomaly is resolved by postulating that social facilitation acts on the motivation to feed, not on the rate of learning directly. A single food delivery to a group of trout excites all the fish present, and they all try to take the food delivered. This rush of feeding activity is the facilitating stimulus for the feeding trout to continue trigger pressing. There is much less evidence for the facilitation acting through any one trout observing another trout pressing the trigger and being motivated to do

the same.

Trained trout which were introduced to the light trigger failed to operate it. They tried to press various parts of it rather than entering between the light and the photocell. To learn to use it thus required the removal of a pressing response and its substitution by a new response. This was beyond the capacity of the trout without some suitable re-training. Naive trout also failed to operate the trigger probably because they were reluctant to enter the confined space between the light and the photocell, and because this is a rather nebulous response compared with trigger pressing. Both problems were overcome by moving a mechanical trigger towards a light trigger and finally removing it. This provided the motivation for trout to enter the light trigger and the necessary re-training for trained trout. The triggers used in the sea cages were light operated, but required a trigger pressing response, so they were not significantly different, as far as the trout were concerned, from mechanical triggers.

Pattern of Feeding.

A diurnal pattern of feeding has been observed in trout (Hoar 1942, Young *et al* 1972) so it was not surprising to see a

dusk peak of feeding activity. Swift (1964) suggests that the dawn and dusk peaks are peaks of activity, and feeding follows as a consequence rather than the other way round. A dawn peak may have been present, but not clear because of variations in light intensity overnight which allowed more or less nocturnal feeding, which in turn affected the degree of satiation at dawn. An appreciable overnight feeding was evident and this was not associated with a high wastage, so the trout were consuming the food delivered. Since the trigger was on the surface and the pellets floated both would be seen in silhouette making feeding possible in the minimum possible light levels. Feeding at low light levels is an established phenomenon in a variety of fish species (Blaxter 1970). With the light-operated trigger there was a continual low level of light in the tank, but results using these triggers were not used for the data on diurnal variation.

A second peak of feeding activity was sometimes noticed at or soon after midnight, about 8 h after the dusk peak. This correlates with the observations of Adron *et al* (1973) who found an 8-h cycle of feeding in continuous lighting, which they attributed to the rate of digestion and stomach emptying. In Pacific salmon *Onchorynchus nerka* of about 30 g the stomach is about 50% empty after 8 h at 10°C

(Brett 1970) and 75% empty after 8 h at 15°C. In rainbow trout fed on dry pellets digestion is a little slower, 40% of the stomach content being evacuated after 8 h at 12°C in 30 g trout (Windell et al 1972) Windell and Norris (1969) consider the time required to saturate dry pellets in the stomach adds significantly to the time of digestion. Brett and Higgs (1970) demonstrated that the rate of stomach evacuation is exponential, being greater when the stomach is full. This means that a subsequent meal which re-fills the stomach will enhance the rate of evacuation of a previous meal.

Unless the trout were actually satiated they were observed to be ready to feed while not actively pressing the trigger. A trial trigger press by the experimenter with a small food delivery would immediately initiate a bout of feeding in these circumstances. This argues for a releasing mechanism in which the continuous discharge of some appetitive behaviour (e.g. trigger pressing and feeding) is prevented by a behavioural block, which is removed by an innate releasing mechanism to allow feeding to occur (Tinbergen 1951, Eibl Eibesfeldt 1970). The releasing factor may be bound up with stomach contents (Adron et al 1973), presence of food, observation of another fish feeding or an admixture of these and other factors. The increased aggregation of

feeds in groups as compared with individuals certainly implicates the presence of other feeding fish in this context, and this has also been demonstrated in birds (Tolman 1967).

A block-and-release mechanism explains the aggregation of feeds. If no such mechanism operated the trout would simply top up with repeated single trigger presses at regular intervals, rather than behave with a fast-and-feast cycle.

Once a feeding bout is initiated the rate of feeding within the bout accelerates, the act of feeding therefore pre-disposes the trout to feed again. This is a positive feedback as described by Wiepkema (1971). Tugendhat (1960) incorporates such a mechanism into her model of feeding in sticklebacks although she does not call it positive feedback.

Rozin and Mayer (1961) found that goldfish did not feed in bouts but at regular intervals throughout the day or night. They used an operant conditioning (demand feeding) technique so food was potentially available at all times. The difference between goldfish and trout is attributable to their different ecology. Since trout are carnivorous a positive feedback is an advantage in that it will ensure a rapid feeding response once feeding is initiated. In this way a carnivorous fish will make the most of whatever

food it finds. Goldfish have no storage stomach so a strong positive feedback is of no great advantage since they have less capacity to gorge themselves, and being non-predatory have less need to take a lot of food as soon as it becomes available.

There is no mention of an initial acceleration of feeding in a number of papers in which feeding was confined to a single daily session (Beukema 1968, Ishivata 1968, Colgan 1973 and Brett 1971). It seems that, since in these cases the fish are deprived of food for 24 h or more, any positive feedback was swamped by the initial surge of feeding activity which is consequent on deprivation. In some cases the hand feeding methods precluded the observation of any positive feedback. An operant conditioning technique allows fish to feed at will, while recording feeds as discrete events and is consequently best suited to study initiation of feeding during relatively normal feeding behaviour. Single session feeding experiments on the other hand are more concerned with satiation within particular experimental regimes.

Positive feedback is of necessity a short lived phenomenon and is soon overcome in a feeding bout by a response to satiation, more specifically to the fullness of the stomach since the amounts eaten to satiation are

constant after a given period of deprivation (Rozin and Mayer 1964, Brett 1971, Ishiwata 1968 a & b). Satiation therefore causes a falling off in feeding rate and its eventual cessation.

Brett (1971) found the time for Pacific salmon fingerlings to feed to satiation was an average of 43 min and was independent of fish size. Ishiwata (1968 c) gives a figure of 60 min for rainbow trout of 135 g at 10°C using hand feeding. When demand feeding the satiation time is about 3 h. It is longer because the rate of food delivery is determined by the fish rather than by the experimenter and there will be periods of several minutes when no food is present in the tanks. In hand feeding more food would be added at this stage and this would be a releasing factor for additional feeding behaviour. Ishiwata (1968 a) gives an equation to predict the way in which the rate of feeding falls off with increasing satiation. I have not tried to fit my data to this equation since Ishiwata took pains to standardise the amount of food deprivation and this factor is entirely variable in a demand feeding experiment.

Evidence from Adron *et al* (1973) suggests trout will re-start feeding when the stomach is about 50% empty rather than entirely empty. Because the rate of feeding is greater with longer periods of deprivation (Tugendhat 1960) satiation

time is not greatly dependent on the fullness of the stomach.

Hierarchy.

Territorial behaviour is well documented in a variety of fish including salmonids. Stringer and Hoar (1955) give detailed descriptions of the behaviour patterns involved. The observation that dominant trout are lighter, in a light tank, than subordinate ones corresponds with that of Newman (1956). He also observed that aggressive behaviour is more marked in smaller tanks. Kalleberg (1958) and Gerking (1953) point out the value of territoriality in a stream, dominant fish occupying areas with good cover and behind stones in slack water, and Keenlyside and Yamamoto (1962) record the importance of food availability in territories. Myrberg (1972) found hierarchies in the bicolour Eupocentrus partitus were linear, each fish having a definite place in the nip order and Brown (1946) observed more marked hierarchichal effects in tanks of 25 trout than in tanks containing greater numbers.

The observation of territoriality in a tank of 5 fish divided by net partitions was not therefore surprising. The lack of such territoriality in a large round tank of 21 trout was due to the absence of physical barriers within the tank, and to the larger number of fish which dilutes out the

hierarchichal effects, particularly since a relatively high density of 2.75 kg/m^3 precluded very much physical separation of the trout.

Whether or not territoriality was observable, hierarchy was a significant feature at all times and was particularly obvious in that a dominant fish did all the trigger pressing. This dominant fish did not occupy a territory to include the feeder in a tank of 5 trout, though it was perforce never very far from it. It would be necessary to have much larger tanks to test this critically. It is clearly the dominant fish with regard to territory which also becomes dominant in terms of trigger pressing. Such fish will assume leadership in a maze (Greenberg 1947) and will probably also assume leadership in investigating the trigger.

If a dominant fish is removed it takes longer for the remaining trout to re-start demand feeding than if the trout are newly introduced to the feeder. This suggests that since the other fish are repressed from using the trigger then this loss of repression, a deconditioning, and the act of learning to use the trigger, a conditioning, take longer than simply conditioning in the first instance.

These hierarchichal effects do not negate the value of demand feeding in commercial fish farming. Provided the reward level is adequate all fish present can take the food

and there was no evidence of deprivation of food to the point where subordinate fish lost condition. It does mean that the total feeding rate is determined by a few individuals but these are by nature more aggressive and are more likely to set a high feeding rate compared to their subordinates.

The sizes of groups used were very small in comparison to the several thousand trout in a tank or pond in a fish farm, so it will be instructive to extend observations on hierarchy to groups of this size. One may anticipate a further dilution in hierarchichal effects with not one, but a group of dominant fish operating the trigger.

Growth, Intake and Food Conversion Efficiency.

With regard to individual trout the considerable variability in conversion efficiency makes it difficult to draw conclusions about intake and conversion. Certainly conversion efficiency is very easily affected by the general behavioural and metabolic state of the trout. It would appear that demand feeding held no advantage over hand feeding twice a day. In the case of groups of trout an advantage in terms of conversion efficiency was found when demand feeding rather than hand feeding once a day. This is of no great commercial significance since very few trout farmers hand feed as infrequently as once

a day, a possible exception being floating cage culture with difficult access. The advantage of demand feeding in improving conversion efficiency would seem to be its relative frequency rather than any of its more subtle features, and this can also be achieved by timed automatic feeding.

Demand feeding does give a very accurate assessment of the trout's preferred rate of food intake. This depends on the reward per trigger press, and a reward level of 0.1 to 0.15% of the aggregate weight of all the fish present gave maximum intake with minimum wastage. This was true of groups of up to 25 trout with a single dominant fish operating the trigger. If, in larger groups, a number of fish operated the trigger then the optimal reward level may be different. A reward level of 0.1 to 0.15% of the aggregate fish weight gave rise to levels of intake in excess of that recommended by manufacturers for optimal conversion efficiency. It is possible to reduce the level of intake by reducing the reward per trigger press, hence demand feeding does not necessarily mean ad lib feeding. This is important in fish farming since ad lib feeding generally gives a low conversion efficiency.

Because of the complicating factors of hierarchy and reward levels a simple demand feeding system in a fish farm

would have to be used with care. A suitable system would be one in which fish demand-fed, but the total daily delivery was kept to the levels suggested in the manufacturers feeding tables by adjusting the reward per trigger press. This would give the advantage of controlled (timed or hand) feeding schedules, with their optimisation of conversion efficiency, plus the advantages of demand feeding in that it is sensitive to the needs of the fish. These may vary through unforeseen circumstances. For example trout in the sea cages have been observed to stop feeding entirely on hot calm still days while on demand feeding, whereas with hand feeding control groups take food. Under these calm hot conditions there may be an oxygen stress which in the absence of daily recordings could go unnoticed by the experimenter or fish farmer.

Floating Cage Culture.

Straightforward once daily hand feeding in the sea cages gave a growth of 1.72% per day in the summer at 14°C and 0.37% per day in the winter at 8°C. Fig 28 shows that the temperature range in Dunstaffnage Bay is 6 to 14°C with a mean of 10°C thus 8°C is average for the winter period and 11°C the temperature used in many of the laboratory experiments is representative of the summer period. It would seem quite

feasible, therefore, to hope for an average growth rate of 1.2% per day from mid-May to mid-November, and 0.47% per day over the winter, although these are necessarily rough estimates.

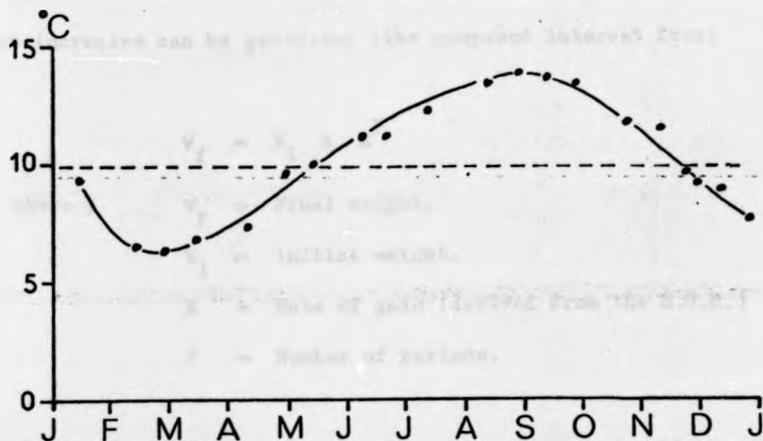


Fig 28. Annual temperature cycle in lower Loch Etive, adjacent to Dunstaffnage Bay. Averaged over 3 years. (Edwards pers.comm.)

The marine phase of trout culture, at least in a partly brackish site, could commence with fish of about 30 g which

become available in November, having hatched in the previous February or March. It has been shown that November is a good time to acclimate fish to sea water since the temperature is falling and rainfall is usually high at this time. A suitable scheme for a fish farm would therefore be to acclimate 30 g trout in November and to market them the following summer. Weight increases can be predicted like compound interest from;

$$W_f = W_I \times R^P$$

where ;

W_f = Final weight.

W_I = Initial weight.

R = Rate of gain (derived from the S.G.R.)

P = Number of periods.

Thus a 30 g fish with a specific growth rate of 0.4% per day over a winter period from November to May (160 days) would reach a weight of;

$$30 \times 1.004^{160} = 56.8 \text{ g}$$

The same fish growing at 1.2% per day for the next 120 days would grow to;

$$56.8 \times 1.012^{120} = 237 \text{ g}$$

This is a suitable market size. One could hope therefore to market the bulk of ones fish in August and September. Appreciable winter growth arises from the relative warmth of the sea in winter, river water falling to much lower temperatures at which trout growth stops entirely.

APPENDIX.

1. RECIRCULATING SYSTEMS.

Spotte (1970) gives an equation derived by Hirayama (1966) to calculate the carrying capacity in recirculating systems.

$$\frac{0.70}{V} \frac{10 W}{950 GD} \cong (B^{0.544} \times 10^{-2}) + 0.051 F \dots 1$$

Where,

W = Area of filter bed (m^2)

V = Velocity of flow through filter (cm/min)

D = Depth of filter bed (cm)

B = Body weight of fish (g)

F = Amount of food entering system daily (g)

G = Grain size coefficient which is given by

$$G = \frac{1}{R_1} y_1 + \frac{1}{R_2} y_2 + \dots + \frac{1}{R_n} y_n \dots \dots 2$$

R_1 = Mean grain size of each fraction (mm)

y_1 = Proportion of each fraction in filter (%)

The left hand term of equation (1) is the "oxidising capacity of the filter bed" (O.C.F.) given in $\text{mgm O}_2 / \text{min}$ and measures in effect the ability of the filter to detoxify the water. The right hand term of equation (1) indicates the rate of "pollution" by the fish and is also expressed $\text{mgm O}_2 / \text{min}$. If the system is to be self supporting it follows that this should be less than the O.C.F.

Hirayama (1966) derived the equation with reference to wet feeding, whereas in this work dry food was also used. This has approximately 1.6 times the calorific value of wet food weight for weight (Freeman et al. 1967). Also since all the fish involved were of similar size the right hand term of equation (1) can be modified to,

$$q (B^{0.544} \times 10^{-2}) + 0.051 \times 1.6F \dots\dots\dots 3$$

$$q (B^{0.544} \times 10^{-2}) + 0.081F \dots\dots\dots 4$$

q = number of fish.

In the initial filter system used in which 2

tanks were supported by two filters, one had a slightly larger pump and the flow rate through the filters (V) were 8 cm/min and 12 cm/min respectively.

The area of the filters (w) was 0.126 m^2 , the depth (D) 16 cm and the grain size coefficient is given by,

$$G = \frac{1}{2.5} \times 93 + \frac{1}{7} \times 7 = 38.2$$

Substituting these values into the left hand term of equation (1) gives O.C.F. values for the filters of 0.77 and 0.78 respectively, or a total of 1.55 for both together.

The final number of fish introduced into the system was 26 fish of 50g each fed a total of 20g of food per day. The food was initially wet food during acclimation. Entering these figures into the equation (3).

$$q (B^{0.544} \times 10^{-2}) + 0.051F$$

gives a value of $3.20 \text{ mgm O}_2 / \text{min}$.

This figure is therefore not exceeded by the

oxidising capacity of the filters (1.55), thus the filters were inadequate. During acclimation, therefore, the water quality was also controlled by siphoning off 1/3 of the volume and replacing it with clean water every two days. Either river water or sea water could be used depending on whether or not it was desired to raise the salinity.

As regards the sub - gravel filter this had an area of 0.5 m^2 and a filtering velocity of 0.5 cm/min. The depth of the gravel was 11.5 cm and the coefficient of gravel size (G) was 33.7. The OCF of this filter, therefore, as given by equation (1) is:

$$\frac{10 \times 0.5}{\frac{0.7}{0.5} + \frac{950}{33.7 \times 11.5}} = 1.50 \text{ mgm/O}_2 / \text{min}$$

This filter system was stocked with up to 10 trout of 40 g fed a total of 6 g dry food per day. Substituting in equation (4) gives:

$$10 \times (40^{0.544} \times 10^{-2}) + 0.081 \times 6$$

$$= 1.23 \text{ mgm/O}_2 / \text{min}$$

Since this is less than the OCF of the filter the system should be self supporting at this stocking density. In practice half of the water volume was replaced weekly.

It was necessary to operate 3 solenoid operated air valves (valves P in Fig 3) from 11.5V a.c. supply. This was achieved by the operation of a second valve (C in Fig 3) after a delay of a few seconds. The circuit diagram was used for this.

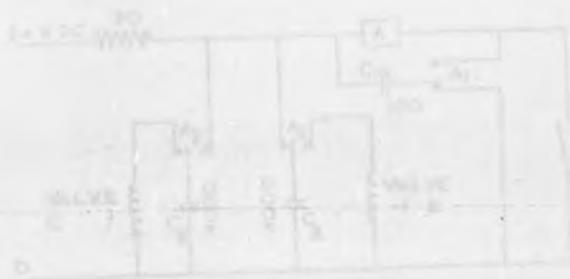


Fig 29. Circuit used to control the air operated feeders. All resistances are in ohms and all capacitances in μF . Valves R and Q correspond to the solenoid operated air valves P and C in Fig 3.

2. ELECTRICAL CIRCUITS USED.

A) Control of compressed air operated feeders.

It was necessary to operate a solenoid operated air valve (valve B in Fig 3 page 10) for a short period followed by the operation of a second valve (C in Fig 3) after a delay of a few seconds. The circuit below was used for this.

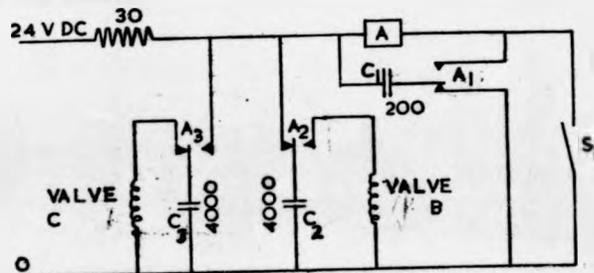


Fig 29. Circuit used to control the air operated feeders.

All resistances are in ohms and all capacitances in μF . Valves B and C correspond to the solenoid operated air valves B and C in Fig 3.

The switch S_1 was associated with the light operated trigger which the fish operated. Its closure energised relay A which was held on for a short time by a 200uF capacitor (C_1) discharging through the relay contacts A_1 . The closure of the relay contacts A_2 discharged capacitor C_2 via the solenoid valve B and caused it to operate. During this time capacitor C_3 charged up. When, after 1 or 2 seconds, C_1 was discharged the relay was de energised and the contacts resumed their positions shown in the circuit diagram and C_3 discharged via valve C to vent off excess air from the feeder.

B. Timing for cine camera.

An electrically operated cine camera was used which could be operated by the closure of a single switch. The switch used was a pair of relay contacts on relay A in the circuit below. It was necessary to run the cine camera for a short time after each trigger press by a trout.

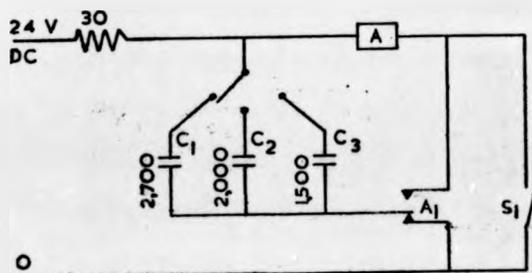


Fig 30. Timing circuit for an electrically operated cine camera. Resistances are in ohms and capacitances in μF .

The switch S_1 , was associated with the demand feeder and its closure activated relay A which was then held on for a period by the discharge of the capacitor C_1 , C_2 or C_3 . These capacitors were selected by a switch and held the relay on for 6, 2 or 1 sec allowing a choice of filming times.

C. Automatic wind on for Exa 11 35mm camera.

The shutter was released by a solenoid operated cable release. This solenoid was energised by a 20,000 uF capacitor discharged when relay A was operated by the closure of switch S_1 which was associated with the switch operating the demand feeder.

The wind on mechanism was initiated by the closure of the flash contacts on the camera (switch S_2) which activated a fast acting relay B, which was held on for a period by a 4,000 uF capacitor operating on one set of its changeover contacts B_1 . A second pair of contacts B_2 switched power onto the 6 V. DC motor to start the wind on cycle. After a short part of this cycle a cam switch S_3 was switched over so that when relay B was de energised the motor continued to derive its power via this switch. When a complete frame was wound on this switch fell into a groove in its cam and switched the motor off. At the same time a second cam switch (S_4) operated relay C which caused a reverse voltage through the motor via contacts C_1 and turned the wind on mechanism back a small distance until this switch was moved by its cam. This small amount

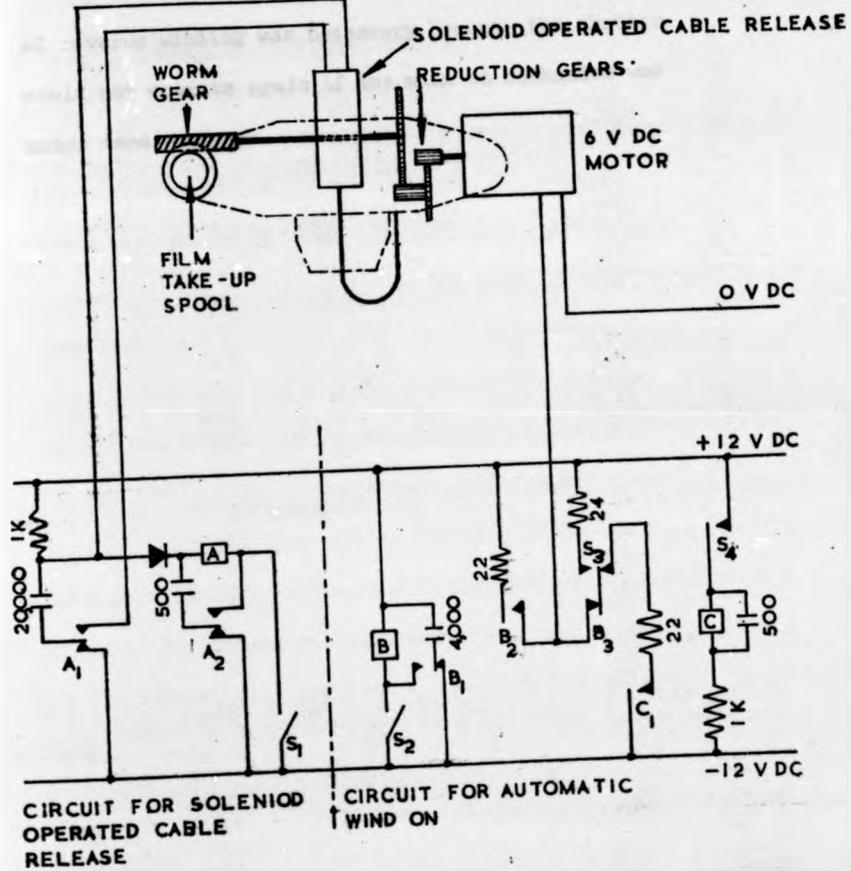


Fig 51. Diagram of automatic wind on mechanism for a 35 mm camera. Resistances in ohms and capacitances in uF.

of reverse winding was necessary because the shutter would not operate again if the wind on mechanism was under tension.

... was provided as a check of the winding
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3. LENGTH AND WEIGHT DATA.

These data are presented as a record of the standard lengths, fork lengths, total lengths and weights which were recorded. They have not been specifically related to the growth curves in the body of this thesis but are presented more to allow relationships to be determined between, for example, the standard length and weight, or the standard length and fork length. While some of these relationships have been used in calculating condition factors, there has been no necessity to use others. The purpose of presenting the data is in case such a necessity should arise in the future. All lengths are in mm and all weights in g .

A) Individuals kept in
56 l tanks.

11.11.71.

Tank	S.L.	F.L.	T.L.	wt
1	200	237	248	182.7
2	215	235	242	149.7
3	235	254	261	201.9
4	220	240	248	146.6
5	258	277	285	271.6
6	254	273	280	296.1
7	243	268	275	244.0

20.12.71.

Tank	S.L.	F.L.	T.L.	wt
1	258	278	286	275.8
2	250	252	260	183.0
3	260	279	288	271.3
4	248	268	276	227.5
5	262	284	291	265.2
6	275	293	230	390.9
7	270	290	295	325.7

12.1.72.

1	273	292	231	299.8
2	235	256	261	188.2
3	274	290	299	291.7
4	255	275	282	223.1
5	262	283	293	253.9
6	278	299	232	383.2
7	278	297	232	318.4

18.2.72.

1	289	320	330	396.9
2	250	270	276	216.4
3	284	307	310	349.3
5	268	290	300	274.8
6	295	316	322	435.0
7	290	310	319	389.8

B) Larger Individuals.

13.4.71.

300	325	334	466.8
290	312	320	390.9
290	310	318	316.8

C) Rainbow trout in
1145 ltank.
10.8.72.

S.L.	F.L.	T.L.	wt	S.L.	F.L.	T.L.	wt
160	171	182	61.5	123	131	139	24.8
162	174	182	60.4	118	126	134	24.3
160	172	180	55.1	120	130	157	23.2
155	165	174	53.6	142	153	161	20.0
156	168	176	53.2	110	119	127	20.0
150	160	170	49.9	111	120	126	19.2
147	159	167	44.1	115	124	130	18.5
134	142	152	44.0	105	115	122	17.3
146	151	165	43.4	104	112	120	16.6
145	155	165	42.8	106	115	120	16.3
144	158	162	42.4	105	114	122	16.2
143	153	161	42.0	105	112	118	15.0
145	155	162	39.9	103	111	116	14.1
139	150	160	37.6				
142	152	162	37.3				
138	150	159	36.5				
139	149	160	35.8				
140	150	159	35.1				
131	141	151	33.1				
132	141	148	32.2				
133	142	152	32.0				
128	135	146	30.6				
124	135	141	29.5				
125	134	143	27.2				
124	134	141	26.6				
123	131	138	26.2				
122	132	139	25.9				
125	135	142	25.0				

24.8.72.

S.L.	F.L.	T.L.	wt	S.L.	F.L.	T.L.	wt
169	181	188	69.3	118	126	135	21.9
165	175	186	62.5	109	117	125	19.5
160	170	178	60.6	110	120	126	18.6
161	173	187	58.7	108	116	124	18.3
149	159	166	58.4	112	123	127	18.0
164	176	138	55.7	108	118	125	16.9
157	169	176	54.2	105	112	120	16.6
156	167	177	52.1	105	112	118	15.6
145	159	165	47.9	105	112	117	14.5
151	161	171	47.9	103	112	120	14.3
150	160	169	44.2				
143	155	165	39.6				
145	155	164	38.1				
142	153	161	38.0				
140	150	160	37.9				
143	154	162	37.8				
140	151	159	35.4				
137	145	155	35.3				
133	143	152	31.9				
133	144	149	31.8				
130	139	145	31.1				
135	145	150	30.5				
130	141	147	29.9				
125	134	145	28.5				
127	133	144	27.6				
125	135	141	27.5				
121	132	140	26.6				
125	135	142	25.2				
123	133	138	23.6				
121	130	138	22.9				

D) Three groups of
rainbow trout.

5.10.72.

Group 1.

S.L.	F.L.	T.L.	wt	S.L.	F.L.	T.L.	wt
190	204	213	104.4	165	177	186	62.7
170	185	194	82.8	160	173	182	58.3
167	180	187	74.4	158	171	180	58.0
162	174	182	68.2	145	155	163	48.8
165	175	187	65.7	158	170	178	44.9
170	184	191	65.2	148	158	165	43.9
167	180	188	62.9	151	165	174	42.8
160	171	182	61.0	116	127	132	32.7
155	165	175	54.8	125	134	143	28.8
151	161	170	50.7	125	135	141	25.5
151	161	170	44.3	124	133	142	24.2
153	165	173	48.0	119	126	135	23.0
145	155	165	46.9				
145	155	163	40.8				
144	155	164	38.8				
138	151	160	36.6				
136	148	156	35.6				
135	146	155	33.9				
109	113	121	14.6				

Group 3.

Group 2.

197	217	227	98.2	156	194	206	92.6
185	200	210	97.8	184	198	206	90.9
181	198	208	89.6	179	193	200	89.6
165	176	186	68.6	178	192	203	88.9
172	186	195	67.9	184	198	208	87.7
166	180	186	64.6	176	190	199	83.8
				170	182	191	74.4
				170	185	192	73.1
				165	177	185	66.7
				151	163	170	53.2
				155	165	175	51.7
				151	162	170	49.4
				146	160	167	43.5

S.L.	F.L.	T.L.	wt	S.L.	F.L.	T.L.	wt
134	141	148	35.2	130	139	146	33.5
140	150	157	33.3	132	143	150	31.0
127	139	148	32.2	129	140	148	30.9
125	134	141	27.4	128	138	144	30.0
123	133	143	25.8	131	140	145	29.5

E) Rainbow trout in sea
cage 1 month after
acclimation to sea
water.

25.8.72.

178	189	199	82.9
175	185	193	71.3
167	178	188	68.6
168	181	190	67.3
166	179	190	64.0
151	161	170	52.2
154	169	174	50.4
150	162	170	50.4
151	165	174	49.1
150	160	170	49.0
147	158	165	46.5
145	156	165	43.4
134	144	151	43.2
141	150	159	40.3
135	145	154	39.7
140	150	160	39.6
140	151	158	37.1
138	148	155	37.0
135	145	154	34.5
138	148	155	34.0

120	133	140	28.8
124	132	140	25.4
118	128	136	25.1
120	130	137	24.7
124	132	164	24.0
109	117	124	17.6

F) Sub sample from sea cages prior to dividing population into 2 equal halves, cage 1 and 2 below.

31.10.72.

S.L.	F.L.	T.L.	wt
238	255	261	252
232	250	256	209
234	247	254	200
238	255	262	198
223	237	246	166
220	235	242	159
212	226	232	156
216	230	241	147
210	225	232	142
203	220	228	140
200	215	223	134
210	225	234	133
198	214	220	133
206	225	231	130
210	226	232	126
201	215	223	107

G) Sample of equal populations in sea cages.

5.12.72.

Cage 1.

S.L.	F.L.	T.L.	wt
245	263	270	230
250	266	275	207
244	262	268	198
230	250	255	193
233	248	255	190
240	258	264	187
236	251	259	180
225	240	247	173
224	240	245	171
223	240	247	161
216	235	243	155
219	235	241	152
215	230	238	151
215	235	244	140
211	230	240	132
216	229	234	132
205	220	226	121
193	208	213	104
196	210	216	101

Cage 2.

252	270	278	244
241	264	272	219
234	250	258	214
239	255	265	212
237	258	264	211
233	250	257	198

20.2.75.

Cage 1.

S.L.	F.L.	T.L.	wt	S.L.	F.L.	T.L.	wt
260	279	287	258	260	278	284	225
247	267	275	244	251	268	274	223
257	278	285	240	233	251	256	220
248	264	273	235	240	260	267	215
258	275	283	232	237	255	262	214
238	255	265	215	240	256	265	205
235	255	261	214	245	258	271	193
235	250	255	209	241	258	265	192
236	255	263	195	228	240	248	180
230	248	255	186	219	238	241	166
226	245	253	176	223	240	248	147
228	245	253	174	208	221	229	119
228	245	254	169	216	260	267	111
230	245	253	165				
216	230	234	163				
224	240	248	161				
220	233	240	154				
215	230	238	146				
195	210	218	105				
185	200	208	92				

Cage 2.

260	174	284	266
253	270	278	253
262	280	288	248
255	275	282	245
255	278	285	241
252	270	278	230
250	265	272	228

H) Three groups of trout
held at 8°C.

5.12.72.

Tank 1.

S.L.	F.L.	T.L.	wt
207	223	233	134
200	216	225	116
206	223	231	112
179	194	201	89
164	175	185	64
164	173	184	64
163	175	184	59
158	170	179	59

Tank 2.

190	196	213	108
195	209	218	105
185	200	208	104
190	204	213	93
168	196	213	74

Tank 3.

245	262	276	246
240	255	262	203
245	265	272	186
230	245	255	179
224	240	246	156
215	230	237	155
220	235	245	151
224	240	246	150
210	227	230	130
204	221	230	125
210	225	234	123

4.1.73.

Tank 1.

S.L.	F.L.	T.L.	wt
213	229	240	140
203	218	226	116
208	225	233	111
183	197	205	91
169	181	187	67
166	175	186	63
163	175	183	61

Tank 2.

205	210	225	120
197	205	212	113
177	188	197	82
186	201	211	76

Tank 3.

248	256	274	247
240	258	266	204
254	271	281	203
238	255	257	188
220	235	241	169
230	245	255	165
231	245	254	163
226	243	251	161
219	235	242	147
210	227	235	134
214	230	236	123

31.1.73.

Tank 1.

S.L.	F.L.	T.L.	wt
220	236	247	155
208	226	235	132
213	230	238	128
181	201	210	102
174	186	194	80
170	181	190	70
165	176	185	67

Tank 2.

210	220	235	136
263	215	222	130
184	195	205	91
182	196	206	65

Tank 3.

248	270	276	249
256	275	283	209
240	258	265	197
235	250	256	188
230	248	255	166
230	244	251	164
230	245	252	159
220	235	245	152
211	228	235	136
210	225	235	116

19.2.73.

Tank 1.

S.L.	F.L.	T.L.	wt
226	243	254	178
217	235	243	152
220	238	245	143
192	206	215	112
180	194	201	91
175	188	196	77
167	177	188	71

Tank 2.

201	222	231	149
205	230	244	149
187	200	212	100

Tank 3.

250	269	276	245
261	280	289	212
245	260	266	201
237	255	251	186
235	251	260	167
231	248	256	162
225	240	248	156
211	230	237	140
211	227	235	114

I) Group of larger trout
in a 1145 l tank.

5.12.72.

S.L.	F.L.	T.L.	wt
240	260	270	199
235	255	263	192
228	246	255	190
228	246	253	184
218	236	246	119
228	245	253	162
228	244	255	155
222	240	248	153
208	225	235	150
210	225	235	145
205	225	230	139
208	235	243	135
205	224	232	135
212	228	236	131
204	219	229	128
200	215	224	125
210	227	234	120
198	214	224	119
198	210	220	118
197	213	220	115
197	211	218	107
191	215	212	104
190	215	225	92

15.1.73.

S.L.	F.L.	T.L.	wt
247	267	273	247
252	271	280	246
258	278	290	244
233	252	256	209
231	251	255	201
240	258	266	190
233	250	261	190
225	241	251	184 ^x
225	241	252	183
225	245	254	182
222	240	250	178
236	255	262	176
226	244	252	164
233	250	262	160
216	234	241	158
210	228	238	153
212	228	235	144
205	220	228	132
217	235	241	128
208	221	232	126
195	220	228	102

19.2.73.

S.L.	F.L.	T.L.	wt
237	255	263	323
262	281	290	309
270	290	300	293
256	280	287	276
243	261	268	244
240	260	269	228
253	270	280	226
245	264	273	217
231	250	260	208
247	264	273	207
232	250	261	202
230	250	257	198
245	261	275	198
230	246	255	197
235	255	263	191
216	235	247	173
221	237	245	164
212	225	234	145
220	237	244	137
198	215	225	104
191	206	216	87

BIBLIOGRAPHY.

- ADRON J. (1972). A design for automatic and demand feeders for experimental fish. *J.Cons.perm.int.Explor.Mer.* 34. 300 - 305
- ADRON J., GRANT P.T. and COWEY C.B. (1973). A system for the quantitative study of the learning capacity of rainbow trout and its application to the study of food preferences and behaviour. *J.Fish Biol.* 5. 625 - 636.
- BEUKEMA J.J. (1968). Predation by the three spined stickleback (Gasterosteus aculeatus). The influence of hunger and experience. *Behaviour.* 31. 1 - 126.
- BLAXTER J.H.S. (1970). Environmental factors - Light - Fishes. In O.Kinne (Ed) *Marine Ecology*, Vol 1, Part 1. 213 - 320. Wiley - Interscience, London.
- BRETT J.R. (1971). Satiation time, appetite and maximum food intake of the sockeye salmon Onchorynchus nerka. *J.Fish.Res.Bd.Can.* 28. 409 - 415.
- BRETT J.R. and HIGGS D.A. (1970). Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon Onchorynchus nerka. *J.Fish.Res. Bd.Can.* 27. 1767 - 1779.
- BRETT J.R., CALAPRICE J.R., GHELARDI R.J., KENNEDY W.A., QUAYLE D.B. and SHOOP C.T. (1972). A brief on mariculture. *Tech.Rep.Fish.Res.Bd.Can.* No. 301 46p.

- BROWN M.E. (1946)a. The growth of brown trout (Salmo trutta Lin.) 1. Factors influencing the growth of trout. J.Exp.Biol. 22. 118 - 129.
- BROWN M.E. (1946)b. The growth of brown trout (Salmo trutta Lin.) 2. The growth of two - year - old trout at a constant temperature of 11.5°C J.Exp.Biol. 22. 130 - 144
- BROWN M.E. (1946)c. The growth of brown trout (Salmo trutta Lin.) 3. The effect of temperature on the growth of two - year - old trout. J.Exp.Biol. 22. 145 - 155.
- BROWN M.E. (1957). Experimental studies on growth. The Physiology of Fishes. M.E.Brown (Ed). Vol 1. 361 - 400. Academic Press, New York.
- CLARK P.J. and EVANS F.C. (1954). Distance to the nearest neighbor as a measure of the spatial relationship in populations. Ecology 35. 445 - 453.
- COLGAN P. (1973). Motivational analysis of fish feeding behaviour. Behaviour. 45. 58 - 66.
- CONTE F.P. and WAGNER H.A. (1965). Development of ionic and osmotic regulation in juvenile steelhead trout, Salmo gairdneri. Comp.Biochem. and Physiol. 14. 603 - 620.

- CONTE F.P. (1969). Salt secretion. In W.S.Hoar and D.J.Randall (Eds), Fish Physiology Vol 1. 241 - 292. Academic Press, New York.
- COWEY C.B. and SARGENT J.R. (1972). Fish nutrition. Adv.Mar.Biol. 10. 383 - 492.
- DAWES B. (1950). Growth and maintenance in plaice (Pleuronectes platessa) Part 1. J.Mar.Biol. Assoc.U.K. 17. 103 - 174.
- DAWES B. (1951) Growth and maintenance in plaice (Pleuronectes platessa) Part 2. J.Mar.Biol. Assoc.U.K. 17. 877 - 947.
- DOUDOROFF P. and KATZ M. (1953). Critical review of the literature on the toxicity of industrial wastes and their components to fish. 2. The metals as salts. Sewage and Industrial Wastes. 25. 802 - 839.
- ETBL - EIBESFELDT I. (1970). Ethology, The Biology of Behaviour. Holt, Rinehart and Winston, New York.
- FREEMAN R.I., HASKELL D.C., LONGACRE D.L. and STILES E.W. (1967). Calculations of the amounts to feed in fish hatcheries. Progve.Fish Cult. 29. 194 - 209.
- GERKING S.D. (1953). Evidence for concepts of home range and territory in stream fishes. Ecology. 34. 347 - 365.

- GREENBERG B. (1947). Some relationships between territory, social hierarchy and leadership in the green sunfish (Lepomis cyanellus). *Physiol.Zool.* 20. 267 - 299.
- GORDON M.S. (1959). Rates of exchange of chloride ions in rainbow trout (Salmo gairdneri) acclimated to various salinities. *Anat.Rec.* 134 571 - 572.
- GORDON M.S. (1959). Ionic regulation in brown trout, Salmo trutta L. *J.Exp.Biol.* 36. 227 - 259.
- GORDON M.S. (1963). Chloride exchanges in rainbow trout (Salmo gairdneri) adapted to different salinities. *Biol.Bull.* 124. 45 - 54.
- HARALSON J. and BITTERMAN M.E. (1950). A lever depression apparatus for the study of learning in fish. *Amer. J.Psychol.* 63. 250 - 256.
- HEMPEL G. (1970). Fish farming, including farming of other organisms of economic importance. *Wiss.Meeresunters., Abt.Helgoland.* 21. 445 - 465.
- HIRAYAMA J. (1966). Studies on water control by filtration through sand beds in a marine aquarium with closed circulation system. 4. Rate of pollution of water by fish and the possible number of fish kept in an aquarium. *Bull.Jap.Soc.Sci.Fish.* 32 20 - 27.
- HOAR W.S. (1942). Diurnal variation in feeding activity of young salmon and trout. *J.Fish.Res.Bd.Can.* 6. 90 - 99.

Hald. A. (1949). Maximum likelihood estimation
of the parameters of a normal distribution which
is truncated at a known point. Skandinavisk
Aktuarietidskrift. 9. 119 - 134

- GREENBERG B. (1947). Some relationships between territory, social hierarchy and leadership in the green sunfish (Lepomis cyanellus). *Physiol.Zool.* 20. 267 - 299.
- GORDON M.S. (1959). Rates of exchange of chloride ions in rainbow trout (Salmo gairdneri) acclimated to various salinities. *Anat.Rec.* 134 571 - 572.
- GORDON M.S. (1959). Ionic regulation in brown trout, Salmo trutta L. *J.Exp.Biol.* 36. 227 - 259.
- GORDON M.S. (1963). Chloride exchanges in rainbow trout (Salmo gairdneri) adapted to different salinities. *Biol.Bull.* 124. 45 - 54.
- HARALSON J. and BITTERMAN M.E. (1950). A lever depression apparatus for the study of learning in fish. *Amer. J.Psychol.* 63. 250 - 256.
- HEMPEL G. (1970). Fish farming, including farming of other organisms of economic importance. *Wiss.Meeresunters., Abt.Helgoland.* 21. 445 - 465.
- HIRAYAMA J. (1966). Studies on water control by filtration through sand beds in a marine aquarium with closed circulation system. 4. Rate of pollution of water by fish and the possible number of fish kept in an aquarium. *Bull.Jap.Soc.Sci.Fish.* 32 20 - 27.
- HOAR W.S. (1942). Diurnal variation in feeding activity of young salmon and trout. *J.Fish.Res.Bd.Can.* 6. 90 - 99.

- HOGAN J. and ROZIN P. (1961). An automatic device for dispensing food kept in a liquid medium. *J.Exp. Anim.Behav.* 4. 81 - 83.
- HOGAN J. and ROZIN P. (1962). An improved mechanical fish lever. *Amer.J.Psychol.* 75. 307 - 308.
- HOLMES W.N. and STAINER I.M. (1966). Studies on the renal excretion of electrolytes by the trout (Salmo gairdneri). *J.Exp.Biol.* 44. 33 - 46.
- HOUSTEN A.H. (1959). Osmoregulatory adaptation of steelhead trout (Salmo gairdneri Richardson) to sea water. *Can.J.Zool.* 37. 729 - 748.
- ISHIWATA.N. (1968). Ecological studies on the feeding of fish. 4. Satiation curve. *Bull.Jap.Soc.Sci. Fish.* 34 691 - 693.
- JENSEN K.W. (1966). Saltwater rearing of rainbow trout and salmon in Norway. *EIFAC Tech.Papers* No.3 43 - 48. J.L.Gaudet (Ed). FAO Rome.
- KALLEBERG H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar and S.trutta L.). *Rept. Inst.Freshwater Res.Drottningholm.* 39. 55 - 98.
- KEENLYSIDE M.H.A. and YAMAMOTO F.T. (1962). Territorial behaviour in the juvenile atlantic salmon (Salmo salar L.). *Behaviour.* 19. 139 - 169.

- KINNE O. (1964). The effect of temperature and salinity on marine and brackishwater animals. 2. Salinity and temperature combinations. *Oceanog.Mar.Biol. Ann.Review* 2. 281 - 339.
- LONGO N. and BITTERMAN M.E. (1959). Improved apparatus for the study of learning in fish. *Amer.J.Psychol.* 72. 616 - 620.
- LONGO.N. and BITTERMAN M.E. (1963). An improved live worm dispenser. *J.Exp.Anim.Behav.* 6. 279 - 280.
- MAITLAND Sir J.R.G. (1887). *The History of Howietoun.* Edinburgh University Press. 278p.
- MILNE P.H. (1970). Marine fish farming in Scotland. *Wld.Fshng.* Sept.1970 46 - 50.
- MUKAI T. (1973). Growth and conversion of rainbow trout reared in brackish and fresh water. *Fish.Bull.* U.S. Dept Commerce. 70. 1293 - 1295.
- MYRBERG A. (1972). Social dominance and territoriality in the bicolour *Eupomacentrus partitus* (Poey). *Pisces: Pomacentridae. Behaviour.* 41. 207 - 231.
- NEWMAN M.A. (1956). Social behaviour and interspecific competition in two trout species. *Physiol.Zool.* 29. 64 - 81.
- NORTHMORE D.P.M. (1968). A simple live worm dispenser. *J.Exp.Anim.Behav.* 11. 617 - 618.

- PALSHHEIMO J.E. and DICKIE L.M. (1966)a. Food and growth of fishes. 1. A growth curve derived from experimental data. J.Fish.Res.Bd.Can. 22. 521 - 542.
- PALSHHEIMO J.E. and DICKIE L.M. (1966)b. Food and growth of fishes. 2. Effect of food and temperature on the relation between metabolism and body weight. J.Fish. Res.Bd.Can. 23. 869 - 908.
- PALSHHEIMO J.E. and DICKIE L.M. (1966)c. Food and growth of fishes. 3. Relations among body size and growth efficiency. J.Fish.Res.Bd.Can. 23. 1209 - 1248.
- PARRY G. (1960). The development of salinity tolerances in the salmon Salmo salar (L) and some related species: J.Exp.Biol. 38 411 - 427.
- PARRY G. (1966). Osmotic adaptation in fishes. Biol.Rev. 41. 392 - 444
- PARRY G., HOLLIDAY F.G.T. and BLAXTER J.H.S. (1959). Chloride secreting cells in the gills of teleosts. Nature. London. 183. 1248 - 1249.
- PENTLELOW F.T.K. (1939). The relation between growth and food consumption in brown trout Salmo trutta. J.Exp.Biol. 16. 446 - 473.
- PHILLIPS A.M. (1969). Nutrition, digestion and energy utilisation. In W.S.Hoar and D.J.Randall (Eds). Fish Physiology. Vol 1. 391 - 432. Academic press, New York.

- RAO M.G. (1971). Influence of activity and salinity on the weight dependent oxygen consumption of the rainbow trout Salmo gairdneri. Mar.Biol. 8. 205 - 212.
- ROZIN P. and MAYER J. (1961). Regulation of the food intake in the goldfish. Am.J.Psychol. 201. 968 - 974.
- SHEHADEH Z. and GORDON M.S. (1969). The role of the intestine in salinity adaptations of the rainbow trout Salmo gairdneri. Comp.Biochem.Physiol. 30. 397 - 418.
- SPOTTE S.H. (1970). Fish an Invertebrate Culture. Water Management in Closed Systems. Wiley - Interscience, New York. 145p.
- STRINGER G.E. and HOAR W.S. (1955). Aggressive behaviour of underyearling kamloops trout. Can.J.Zool. 33. 148 -160.
- SWIFT D.R. (1964). Activity cycles in the brown trout (Salmo trutta L.). 2. Fish artificially fed. J.Fish.Res.Bd.Can. 21. 135 - 138.
- TINBERGAN N. (1951). The Study of Instinct. Oxford University Press.
- TOLMAN C.W. (1967). The feeding behaviour of domestic chicks as a function of the rate of pecking by a surrogate companion. Behaviour. 29. 57 - 62.

- TUGENDHAT B. (1960). The normal feeding behaviour of the three - spined stickleback (Gasterosteus aculeatus). Behaviour. 15. 284 - 318.
- VINCENT R.E. (1960). Some influences of domestication upon three stocks of brook trout (Salvelinus fontinalis Mitchell). Trans.Am.Fish.Soc. 89. 35 - 52.
- WELTY J.C. (1934). Experiments in group behaviour of fishes. Physiol.Zool. 7. 85 - 128.
- WIEPKEMA P.R. (1971). Positive feedbacks at work during feeding. Behaviour 39. 266 - 273.
- WINDELL J.T. and NORRIS D.O. (1969). Gastric digestion and evacuation in rainbow trout. Progve.Fish.Cult. 31. 20 - 26.
- WINDELL J.T., HUBBARD J.D. and HORAK D.L. (1972). Rate of gastric evacuation in rainbow trout fed three pelleted diets. Progve.Fish.Cult. 34. 156 - 159.
- YOUNG A.H., TYTLER P., HOLLIDAY F.G.T. and MacFARLANE (1973). A small sonic tag for measurement of locomotor behaviour in fish. J.Fish Biol. 4 57 - 65.

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