THE ROLE OF PREY SIZE IN THE FEEDING BEHAVIOUR

AND GROWTH OF JUVENILE ATLANTIC SALMON (Salmo

salar L.).

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SUMMARY

The distribution and behaviour of juvenile Atlantic salmon (Salmo salar L.) in a selection of river and stream habitats was studied with particular reference to feeding behaviour. It was concluded that salmon fed predominantly on drifting material. Drift feeding behaviour was studied using a recirculating flume tank simulating a simplified stream environment. The effect of prey particle size on the distance of first reaction, striking, and selectivity was investigated. Reaction distance was maximal on prey whose diameter was 0.025 fish length (fl), and striking distance was maximal on prey of 0.025 to 0.051 fl, and both decreased on larger and smaller prey. 100% of available prey of diameter 0.025 fl and less were ingested, while 90% of 0.051, and 100% of 0.105 fl prey were rejected. Head and jaw movements involved in capture, manipulation, ingestion or rejection of prey were studied, as a result of which mouth breadth and gill raker spacing were proposed as morphometric limitations on the maximum and minimum accessible prey size respectively. On this basis the relative range of accessible prey sizes remained constant at 0.06 fl, irrespective of fish size (2.8 to 20.3 cm length). The effect of prey size on the growth of salmon from first feeding alevins to second year smolts was investigated. Alevins were found to show a good growth rate on all prey of diameters from 0.0115 to 0.090 fl. In contrast all other fish sizes (4.2 to 20.3 cm) showed maximum growth rate on prey of diameter 0.022 to 0.026 fl, although some seasonal variation was indicated. Reaction, strike and selectivity behaviour corresponded with growth response and the proposed morphometric limitations. Results are discussed in relation to vision, behaviour, functional morphology and growth in general and a composite scheme drawn up.

CONTENTS.

PREFACE

In order to meet the dietary requirements of an animal both of the following factors must be considered (i) nutritional components of the diet and (ii) physical and biological characteristics of individual prey items governing accessibility to the predator and determining the energy expenditure during feeding and net energy gain. Much work has been done on the nutritional requirements of certain fish species, which is in contrast to the small amount of information available on prey accessibility. The work that has been done in the latter field falls broadly into three categories:

(i) Ecological approaches to natural predator-prey systems predominantly by predator stomach contents analysis.

(ii) Behavioural approaches in the form of selectivity and preference experiments.

(iii) Growth experiments using natural or artificial diets.

Approaches to the problem outlined in the first category suffer from several serious drawbacks which preclude the determination of the characteristics of prey items which influence accessibility. Stomach contents reflect the particular local and seasonal composition of prey populations, their analyses suffer from severe errors only rarely corrected in the published literature, and confound preferences for particular species of prey with selection for particular fundamental characteristics, e.g. prey body size. The almost complete lack of agreement between work carried out by different authors is indicative of the problems associated with this sort of empirical approach (see Chapter 3). In any case stomach contents analysis can provide no information on prey optima that would be shown in the absence of environemtal constraints present at the time of sampling. Experiments investigating selectivity behaviour (ii) on natural prey similarly introduce the problem of species linked preferences. The interpretation of results of such experiments and of stomach contents

analysis requires the definition of the interrelationships between all
of the characteristics of prey affecting selection: an almost impossible
task.

Growth responses to particular diets have been studied to a limited
extent, almost exclusively within the fish feed manufacturing industry.
Unfortunately the resulting diet has been predominantly determined by
production techniques rather than the absolute requirements of the fish.
Thus, for example, the availability of commercial diets in grades that
are linked to the size of the fish gives limited, andpossibly misleading,
information on the optimum size of particle for a particular size of fish.

In order to construct a general scheme describing the accessibility
of prey it would be necessary to define all the characteristics of all
the known prey of a particular fish species prior to their experimental
investigation. Due to the complexity of form and composition of natural
prey items this is not really feasible, and in any case a phenomenal
amount of experimental data would be required in order to isolate
individual components. However the problem can be approached differently
by using simplified prey possesing a few clearly defined and manipulable
characteristics. It would therefore be a simple matter to vary one (e.g.
colour, size, shape) while keeping all others constant, eventually
building up a composite scheme. Such a scheme could be verified using
limited and specific experiments with natural prey.

The relationship between predator size and prey size is of over-
whelming ecological importance (frequently cited as the cornerstone of
niche-separation, and invading species success for example) and therefore
forms a logical starting point.

Efficient foraging demands adaptation to a particular size-spectrum
of prey, the selection of which is a function both of evolved feeding
behaviour and the functional morphology of the food-gathering system of
the predator. Successful food-acquisition generally results in growth,
thus it follows that the accessible prey-size spectrum and its optimum

can be investigated by means of growth response to particular prey sizes. Since feeding behaviour, functional morphology, and growth are closely interrelated it is clearly important to study all three aspects and interprete the results collectively.

The Atlantic salmon (<u>Salmo salar</u> L.) is an important fish species both from the commercial and recreational point of view. Commercially it is fast becoming a major component of the aquaculture industry while the hatchery supplementation of natural stocks exploited by commercial and sports fisheries has long been an established practice. Since juveniles play a key role in both forms of exploitation an understanding of their dietary requirements is of crucial importance. Within the aquaculture industry the presentation of an artificial diet in an optimally accessible form is of obvious commercial value. Similarly the efficient management of salmon as a resource demands a knowledge of optimal dietary requirements. While clearly the natural prey spectrum of salmon is more variable than that under the experimental conditions reported herein the definition of underlying principles governing prey size accessibility is fundamental to understanding predation and growth in the wild. It is a fact that natural prey populations are manipulable and the provision of sufficient prey of a particular size range could be of importance in cases where an enhanced growth rate is desirable.

CHAPTER I

Feeding and associated behaviour in the wild.

Contents:

INTRODUCTION

The territorial and feeding behaviour of those juvenile salmonids that spend all or part of their lives in freshwater streams has been investigated by Lindroth (1955), Stringer & Hoar (1955), Newman (1956), Kalleberg (1958) Chapman (1962), Keenleyside (1962), Keenleyside & Yamamoto (1962), Chaston (1968), Jenkins (1969) and Mason (1969).

As part of the authors' research into the feeding behaviour of juvenile Atlantic salmon (Salmo salar L.) it was necessary to obtain information from the "wild" environment in order to relate laboratory experimental design and results to the fishs' unmodified behaviour. Bearing in mind the existing information and its shortcomings it was decided to use SCUBA diving techniques to permit underwater observation with maximum observer flexibility. Use of diving to obtain this sort of information is by no means new. Keenleyside (1962) and Keenleyside and Yamamoto (1962) used snorkelling in order to study the behaviour of Atlantic salmon and brook trout (Salvelinus fontinalis). The development and increased availability of SCUBA technology has resulted in further extensive studies notably those of Hartman (1965), Gibson (1966), Edmundson et al (1968), Everest and Chapman (1972). As far as the author is aware there is no published information of a corresponding nature on Atlantic salmon from habitats within which the species co-exists with brown trout (Salmo trutta).

Tinbergen (1957) defines territory as "the result of the two tendencies of the owner, viz., attachment to the site and hostility to a certain category of other animals, usually members of the same species". He considers that its functions are to assure the holder certain advantages together with their exclusivity. Juvenile salmonid territories are primarily feeding territories maintained by a repertory of agonistic behaviour which can conveniently be divided into three categories:

1. Direct aggressive responses (approaches and direct attack)

2. Ambivalent or threat responses (those postures and movements that have an intimidating effect, usually of a complex and

formalised nature during which all other activities cease)

3. Escape responses (including submissive and appeasement acts
   i.e. avoidance responses)

(Chiszar, Drake & Windell 1975 after Jenkins 1969). Changes in eye and
body colouration or colour intensity may well act as non-aggressive
reinforcers of a previously established dominance heirarchy (Keenleyside
& Yamamoto 1962).

The food of stream dwelling salmonids is either of benthic or
terrestial origin. At any one site the available food spectrum can be
split into three discrete groupings; the substrate, suspended drift, and
surface (terrestial) drift. The upstream origin of drift material means
that its abundance is largely independent of local productivity. Drift
prey abundance (i.e. amount per cross-sectional area of water flow per
unit time) within a single habitat increases in proportion to current
velocity (Chapman & Bjornn 1969). While the benthos and surface drift
have discrete faunal composition the suspended drift contains material
originating from both sources. Salmon and trout are known to make use of
both sources and all three groupings of food material[*] (Allen 1941, 2,
Muller 1954, Nilsson 1957, Thomas 1962, Hunt 1965, Egglishaw 1967,
Elliot 1967, Chaston 1968, and 1969, Tusa 1969, and Metz 1974).

Substrate and drift feeding imply the use of two feeding behavior
patterns, the location and capture of immobile or slowly moving organisms
amongst the substrate, or of fast moving material carried within the
water current (and often at some distance from the fish). It was the
purpose of this investigation to examine feeding behaviour in natural
unmanipulated habitats with particular reference to position choice
within the horizontal and vertical current profile, association with the
substrate, feeding mode (as outlined above), and actual capture behaviour.

[*] There is evidence that salmonids feed on flying insects above the water
surface (e.g. Kalleberg 1958). This was not seen during the present
study but no observations were made at dusk when such insects tend to
swarm.

As the maintenance of territory is inextricably involved with feeding a consideration of this and associated agonistic behaviour is inevitable.

Within any habitat there exist good and poor feeding sites (be this a function of prey abundance or accessibility) which will be reflected by the microdistribution of an animal seeking to maximise food intake. The problem of microdistribution of juvenile salmon within substrate and water flow complexes has received scant attention in the literature, and therefore close attention has been paid to the microhabitat (Baldes and Vincent 1969) occupied by the animal while feeding. "Station" is defined as "the place where an occupant of a territory mainly stays, and where it also displays the maximum of aggressiveness" (Kalleberg 1958). The "forage space" represents the maximum extent at which prey capture takes place but which is repeatedly used during the period of observation.

METHODS

All observations were carried out using compressed air SCUBA
diving equipment, except for preliminary site exploration which was
sometimes done using a snorkel. Neoprene wetsuits were always worn.

Observations were recorded as they were made using either submersible
electronic recording equipment or suitable writing boards. The recording
apparatus consisted of a cassette tape recorder within a waterproof case
strapped to the divers back (or carried) connected to a bone microphone
inserted under the wetsuit hood against the temple. A mouth box was used
rather than a conventional mouthpiece. Transcripts of recordings or
notes were made after each day's dives.

It was soon found that a diver lying or moving above the fish
caused violent escape and hiding reactions and that even after apparent
habituation to his or her presence fish rarely did more than try to maintain
position close to the substrate. However a diver proceeding slowly along
the substrate could approach to within 0.5 to 1.0 m of individual fish
before they moved off. During the high temperature periods (June to August)
fish would return within a few seconds to their former position and
activity. If the observer approached closer it was possible to displace
fish from their station but they would frequently swim around the diver,
approaching the faceplate and sometimes attacking a hand trying to displace
them. If the diver rose to the surface escape/hiding reactions would
then occur as above.

A technique was adopted therefore wherein the observer proceeded
slowly upstream (using convenient rocks or a previously anchored rope where
current velocities were high) as close to the substrate as possible, while
continually recording observations. Pauses for detailed observations and
measurements were made as necessary. Observation periods were between
10.00 and 12.00 hrs and 14.00 and 17.00 hrs British Summer Time.

Distances underwater were measured using a 50 cm ruler or 2.5 m rods
graduated in 10 cm divisions. Fish lengths were estimated by comparison

with the ruler and objects of known size. The accuracy of these estimations was verified in an aquarium tank.

Preliminary species identification was always checked by at least one, usually two, other divers. In one or two cases positive identification was impossible without capture of the fish and so was not undertaken. This is indicated where applicable. Identification of fish under 7-8 cm in length in any case proved impossible and these have been labelled as salmon or trout purely on the basis of the results of previous work undertaken by the staff of the Freshwater Fisheries Laboratory on the water body in question.

Current velocity profiles were taken using a Watts Helix current meter held on a graduated extension pole, except at site D where a T.S.K. hand-held meter was used. Both systems give velocities integrated over time, hence avoiding inaccuracies due to short-term local turbulence. Particular attention was paid to measuring velocities at the observed feeding stations. Velocity measurements were obtained also by determining the time taken for suspended material to pass over a known distance. Although profiles and single point velocities could not be obtained by this method it was found to be a good check on the accuracy of flow meter measurements.

Water temperatures were taken at the site using a thermometer held in the main current flow. Weather and air temperature data was provided by the Department of Agriculture and Fisheries for Scotland.

In order to be certain of obtaining meaningfull information it was decided to study a selection of habitats rather than concentrate on an in-depth study of one. Observations were repeated at several sites in order to assess changes with time. It soon became clear that deep slow-moving or static water, particularly if associated with silt or mud substrates did not support resident salmonids. The range of useful habitats studied was thus confined to faster flowing waters with coarser substrates, those in which salmonids were not found are not reported on

here.

Drift sampling using tube-type 400 micron mesh net samplers was accomplished at site C on 24th May, and at site B on 14th June 1977.

FIG. 1   Location of Sites, for further details see text and Table 1.

TABLE 1 - Sites, periods of observations and environmental data

Site	Date (1976)	Time	Weather	Max. & Min. Air Temperature At Faskally Degrees C	Water Temperature At Site C
A. Tay (Logierait)	29 June	am	clear, very sunny	26.0- 9.4	18.0
	02 Aug	am	clear, very sunny	27.0-13.5	17.0
	15 Sept	pm	variable, cloudy	13.0- 6.0	10.0
	*16 Sept	am	variable, cloudy	13.0- 3.0	10.0
B. Tummel (Pooltreigh)	29 June	pm	clear, very sunny	26.0- 9.4	18.0
	02 Aug	pm	clear, very sunny	27.0-13.5	17.0
	13 Sept	am	overcast, rain	15.5- 6.0	9.0
C. & c. Girnaig	30 June	pm	cloudy	18.0- 9.4	17.0
	05 Aug	am	clear, sunny	25.0-11.0	14.5
	14 Sept	pm	mainly cloudy	15.0- 8.0	9.5
D. Garry	03 Aug	pm	clear, sunny	27.0-14.0	15.0
	14 Sept	pm	mainly cloudy	15.0- 8.0	9.5
E. Linn of Avon	01 Aug	pm	variable, some sun	24.0-14.0	11.5

TABLE 1 - Sites, periods of observations and environmental data (contd)

Site	Date (1976)	Time	Weather	Max. & Min. Air Temperature At Faskally Degrees C	Water Temperature At Site C
a. Tay (Dalguise)	13 Sept	pm	overcast, rain	15.5- 6.0	9.0
b. Tummel (Pitlochry)	14 Sept	am	mainly cloudy	15.0- 8.0	9.5

NOTES:

* No diving observations - electric fishing only

  a, b, c - subsidiary sites, see text.

STUDY AREAS

Sites were chosen to provide a reasonable cross-section of habitats in which salmon and/or trout were known to be present. All were on the upper reaches of the Tay river system (Fig. 1), except for site E which was on a tributary of the River Spey.

Site A - Tay at Logierait

Site A was 61 m above mean sea level (MSL) and had a gently graded gravel and rock substrate. A series of stable gravel ridges extended across the river at a frequency of 8 to 20 m (crest to crest) and lay exposed near the shore. Water depth at mid-stream was 0.6 m at ridge crests with a maximum of 1.5 m depth between them. River width at the site was 80 to 100 m and surface velocities were in the region of 0.6 to 0.8 m sec^{-1}.

In general the leeward side of each ridge was composed of fine gravel and small rocks (plate1) with no vegetative cover while the troughs between and the upstream sides of ridges were densely overgrown with Myriophyllum, Fontinalis and Callitriche plants. Strands of Myriophyllum overhung the ridge crest in the current. Plates 1 and 2 show a typical ridge lee slope and crest and the type of plant cover in the trough. The turbulence created by each ridge resulted in a space along its lee within which current velocity was very low (less than 0.05 m sec^{-1}) and flowing in the opposite direction to the main flow. There were pockets of static water amongst the plant material in the troughs.

Site B - Tummel at Pooltreigh

The site at Pooltreigh was at 76 m above MSL, about 2km downstream of the town of Pitlochry and about 3 km below the dam at Faskally. The substrate consisted of gravel and rocks with larger rocks and boulders in deeper pools. Plate 3 was taken at a different site but gives a good idea of the type of substrate found here. Most rocks were in the 3 to 8 cm size range, interspersed with material 0.5 to 1.5 cm in diameter. The largest boulders were about 100 cm in diameter but most were considerably smaller. Observations were made along a transect at the point where separated water flows converge after passing an island. River width was about 80 m, over

half of which was 0.8 m deep and the rest shelved to a deep pool 3 to 4 m
deep near one bank. Water flow was confined mainly to the centre of the
river (where it reached a surface maximum of 1.4 m sec^{-1}) and the deep
pool. Further upstream and downstream depths increased to over 2 m.
Limited algal growth provided the only plant life at this site.

Site C - Girnaig

Site C was a small pool at 284 m above MSL immediately downstream
of the confluence of the main stream of the Girnaig and a side stream.
The substrate was mainly bedrock with large rocks and coarse gravels
(Plate 4). The pool was oval in shape, 6 m long with a width and maximum
depth of 1.5 and 0.4 m respectively at the head, increasing to 5.0 and
1.0 m at the centre and decreasing again to 4.5 and 0.75 m at the tail end.
Half of the width was less than 0.15 m in depth with a substrate composed
of loose rocks. Water current velocity varied from 0.6 m sec^{-1} to zero
depending on depth and width.

Site D - Garry at Killiecrankie

Site D was within the deep gorge at the Pass of Killiecrankie at
about 107 m above MSL. In the gorge the river was about 2 to 3 m deep
and 15 m wide with a rock and gravel substrate and almost imperceptible
current. However at the actual site there was a constriction reducing the
width to 10 m and depth to 0.5 m. The resulting current reached a maximum
surface velocity of 1.05 m sec^{-1}. The substrate was similar to that shown
in Plate 3 although the river banks were vertical bedrock and one or two
bedrock outcrops intruded into the water flow almost to the surface.

Site E - Linn of Avon

The lowermost of a series of pools and small waterfalls at Linn of
Avon was chosen as site E, which was 427 m above MSL. The main part of the
pool was about 35 m in length with a maximum width of 25 m. The substrate
was composed of fine gravel and mixed rock sizes (Plate 5). Towards each
edge of the pool the mean substrate particle size became smaller until
only the finer material (between the rocks in Plate 5) remained, shelving

gently to the surface. Mid-pool was 1.5 m deep, reducing to 0.5 m at the

pool tail. The current was very localised along the central axis of the

pool reaching a maximum of 0.4 m sec^{-1} at the tail. The water was

characterised by extremely good visibility in excess of 18 m due to a low

concentration of suspended material.

Fig. 2 presents the vertical current velocity profiles found at the

sites.

PLATE 1. Logierait site A. View looking upstream onto ridge lee
slope. The distance from foreground to ridge crest
(arrowed) is 1.5 m. Note predominantly gravel substrate
and _Myriophyllum_ fronds overhanging slope.
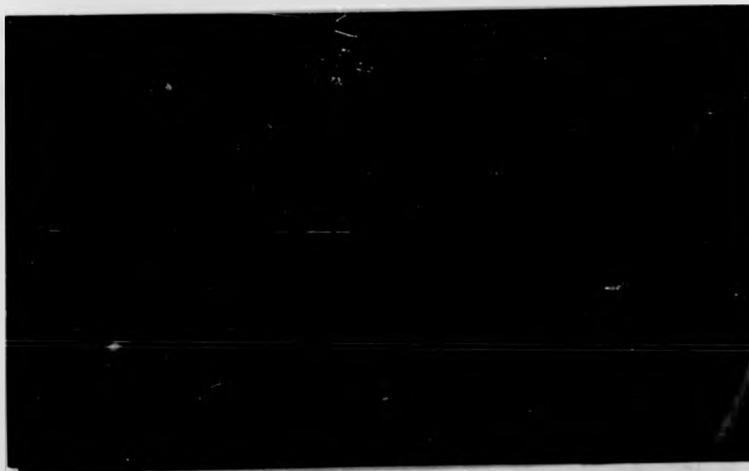
PLATE 2. Logierait site A. View across current stream looking along
trough. Markings along pole are at C.10 m intervals.
Callitriche and _Fontinalis_ in foreground, _Myriophyllum_
plants cover remainder of substrate.
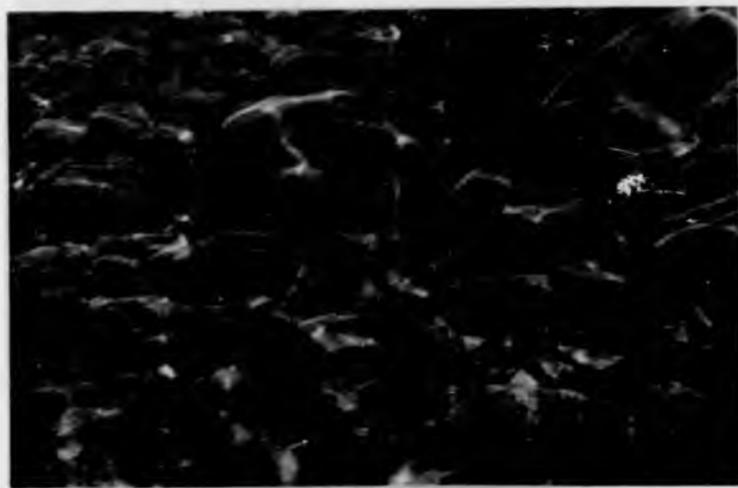
PLATE 3. Pooltreigh site B. Example of type of substrate found
at this site, although larger rocks at top right were
much less frequent than would appear from this photo-
graph. Large rock in centre is 25 cm across. Note
restricted distribution of particle size and absence of
fine material.
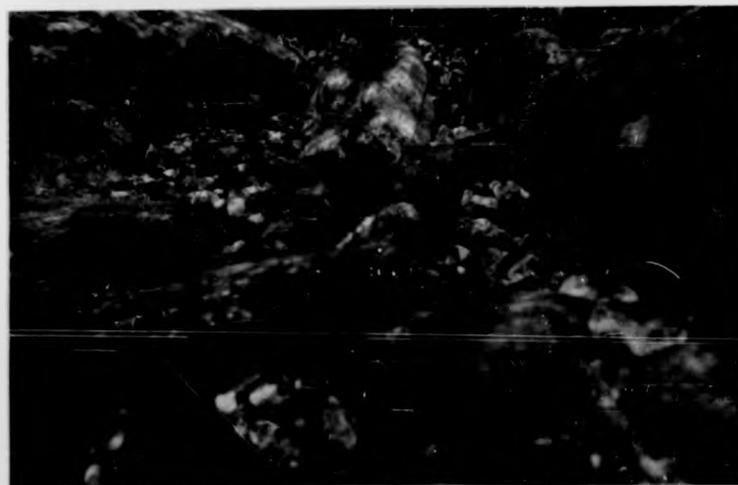
PLATE 4. Girnaig site C. View upstream showing substrate at this
site. Fish in centre (arrowed) is about 12 cm in length.
Note bedrock in top left and settled drift material
deposited in its lee. Substrate size distribution is
typical of this site, smaller sizes decreasing towards
head of pool, increasing towards tail.

PLATE 5. Linn of Avon site E. Photograph shows typical substrate
at this site. Fish (arrowed) on central rock is 3 cm in
length. Substrate can be seen to be composed of rocks
intersperced with fine gravels. Note accumulation of
detrital material.

PLATE 6. Fish (about 5 cm in length) showing characteristic
posture, holding station just above substrate. Note
extended pectoral fins.

FIG. 2(a). Vertical current velocity profiles.

Top : Logierait site A, above ridge crest.
Centre : Pooltreigh site B, mid stream.
Bottom : Garry site D, 2 m off bank.

Current   Velocity   (m sec⁻¹)
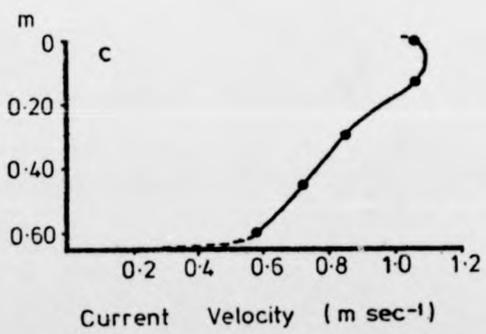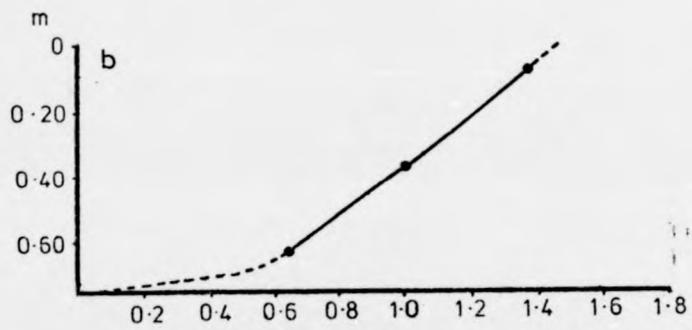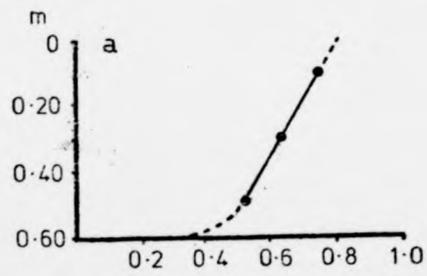
FIG. 2(b). Vertical current velocity profiles.

Top : Girnaig site C[*]
     (1) mid stream at tail of pool
     (2) mid stream at centre of pool.
     (3) mid stream at confluence of streams.
     (4) mid stream at head of pool.

Bottom : Linn of Avon site E.
     (Left) mid stream at tail of pool.
     (Right) mid-way between above and bank.

[*] Pool level raised 0.2 m after June observations,
prior to current velocity measurements at this site.

(a) m
    0
    0·20
    0·40
    0·60

(b) m
    0
    0·20
    0·40
    0·60

(a)

m

1   2   3   4

(b) m

Current   Velocity   (m sec⁻¹)
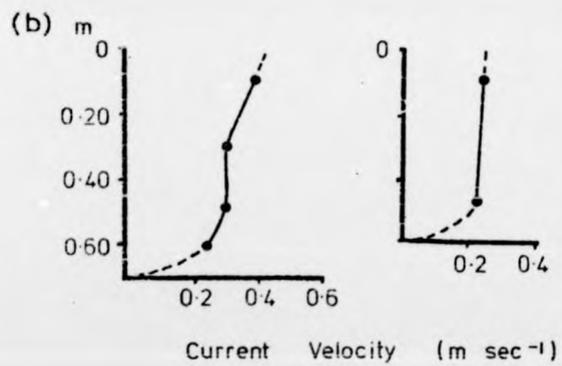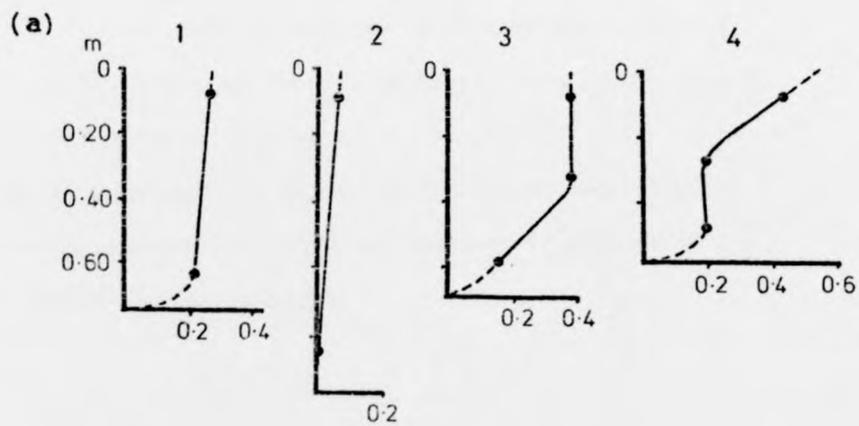
RESULTS AND DISCUSSION

Species distribution.

Salmon were the predominant juvenile salmonid found at the sites (Table 2). There is some evidence that salmon and trout occupy different habitats during their early life (Lindroth 1955). Sub-surface observations in inshore, shallow water at sites A and B failed to locate any trout. Gardiner (pers. comm) reports the results of electric fishing in water up to 0.5 m deep inshore on the Tay at Logierait and Tummel at Pooltreigh and Pitlochry where trout juveniles were found but represented only 3% of the total 0+ salmon and trout caught.

TABLE 2 - Species Distribution.

(Excluding observations during September)

SITE	SALMON JUVENILES		TROUT JUVENILES	
	0+	1+ & older	0+	1+ & older
Tay (Logierait) A	X	X		
Tummel (Pooltreigh) B				
lower mid-water		X		
substrate	X			
Girnaig C				
pool head		X		X
pool tail		X		
Garry D		X		
Linn of Avon E	X	X	X	X

N.B. 0+ fish are those taken to be in their first season of growth
(i.e. first year since hatching), likewise 1+ signifies fish
in their second season.

Microhabitat choice and microdistribution.

Table 3 is a summary of fish size/density/current velocity and association with substrate. In all the sites studied fish were found to occupy some areas in fairly dense concentrations (up to 3 fish m^{-2}) while the greater part of each river and stream (referred to collectively as streams from this point on) held few resident fish. Densities varied considerably both from site to site and with time. This variation probably reflects food availability and overall carrying capacity of different streams as well as variations in food and space requirements with fish size (Allen 1969). These points will be considered under the relevant sections.

Concentrations of fish were only found either in or adjacent to the fastest locally available current velocity. For example at site D a 5 m length of stream at the constriction held 40 to 50 fish while only 12 fish could be found throughout 300 m of stream downstream of this high velocity area. Fish of total length of 7.0 cm and less however consistently held stations out of the major water flow, avoiding continual exposure to high current velocities, and utilising available shelter in the lee of a ridge (A) or remaining amongst or within 0.05 m of the substrate where a substantial current velocity reduction occurs (Fig.2). The fish adopted the posture shown in Plate 6 and described by Keenleyside (1962) whereby position is maintained by using the pectoral fins as hydroplanes in order to remain near or maintain contact with the substrate. Both Kalleberg (1958) and Hartman (1963) have shown that increase in current velocity caused fry to move closer to the substrate and also make greater use of eddies caused by rocks or other objects. It has also been demonstrated that atlantic salmon parr become less bouyant with increasing current velocity (Neave et al 1966 and Pinder & Eales 1969).

TABLE 3 - Microdistribution data, arranged in order of fish size.

FISH LENGTH cm	FISH AGE yrs	SITE	LOCAL FISH DENSITY fish/m²	CURRENT VELOCITY AT STATION m/sec	bls*	DISTANCE OF STATION ABOVE SUBSTRATE m	DATE
3.0	0+	E	0.3-1.2	0.20	6.7***	on or amongst	1 Aug
4.0	0+	B	4.0-6.0 **	0.20	5.0***	on or amongst	29 June
5.0	0+	A	-	0.00	0.0	on and above	29 June
7.0	1+	E	0.3-1.2	0.30	4.3***	on or amongst	1 Aug
8.0	0+	B	0.5-0.8 **	-	-	on or amongst	2 Aug
8.0	1+	C	1.0	0.20	2.5	0.05 - 0.10	30 June, 5 Aug
12.0	1+	B	0.06 **	1.00	6.7	0.15 - 0.25	29 June, 2 Aug
12.0	1+	A	1.0	****	****	on and above	29 June
12.0	2+	C	2.0-3.0	0.40	3.3	0.01 - 0.40	30 June, 5 Aug
12-15.0	1+/2+	D	2.0-3.0	0.90	6.0	0.10 - 0.50	3 Aug

Notes: Body lengths sec^{-1}
** But 1+ fish territories distributed directly above 0+ territories.
*** Maximum current velocity fish were exposed to while feeding. The station was held on or amongst the substrate and subject to local velocity variations which could not be measured. At site B the figures given was estimated.
**** Current velocity virtually imperceptible.

It is of interest to note that fish of about 8.0 cm in length
at site C remained in an area of relatively low velocity (less than
0.20 m sec^{-1}) at the tail end of the pool although, judging by the
high concentration of actively feeding fish at the head of the pool,
this was clearly an inferior site. Social dominance by the considerably
larger (12.0 cm) fish at the pool head may have been responsible for
restricting these fish to the pool tail. There was much non-utilised
space in the 6 m long slow-flowing region seperating these two groups
of fish.

The largest fish (12.0 to 15.0 cm in length) at all sites,
except in a few cases where fish maintained an aggregative social
structure, held stations off the substrate and within water velocities
of between 0.40 and 1.00 m sec^{-1}. The only exception to this was at
site A where local topography allowed the residents to make use of a
0.40 to 0.80 m sec^{-1} current velocity while maintaining a resting
station outside of it.

The concentration of juvenile salmonids in areas of high current
velocity, for example riffles as opposed to pools, and the increase in
the current velocity component of the microhabitat with increase in the
size of the fish appears to be a general characteristic of stream-
dwelling salmonids (Lewis 1969, Jenkins 1969, Saunders and Gee 1964,
Chapman and Bjornn 1969, Everest and Chapman 1972).

The fish 12.0 cm in length observed maintaining position in a
current velocity of 1.00 m sec^{-1} must have been swimming at a sustained
velocity equivalent to 6.7 fish body lengths sec^{-1} (bls). Table 4
lists comparative swimming velocity data obtained from laboratory work
and indicated that such high sustained speeds are characteristic of
other juvenile salmonids. Gibson (1966) reports Atlantic salmon parr
(of unspecified size) maintaining position in current velocities as
high as 1.15 m sec^{-1}, and Symons (1976) found Atlantic salmon juveniles
4.42 to 12.28 g in weight probably in the ≈ 5.0 to 9.0 cm size range)

TABLE 4. Comparison of sustained swimming velocities found in salmonids.

Species	Velocity body lengths sec^{-1}	Fish length cm	Temperature degrees C	Source
Salmo gairdnerii	3.0-4.7	19.3	10-20	Dickson and Kramer 1971
Onchorhynchus nerka	6.7	7.7	15	Brett and Glass 1973
	4.2	12.8	15	
	8.2	5.5	20	
Onchorhynchus kisutch	7.3	4.0	18	Glova and McInerney 1977
	5.5	12.0	18	

predominantly selecting velocities between 0.30 to 0.49 m sec^{-1}.
Unfortunately it is not clear whether fish were free-swimming or
associated with the substrate, or if these positions were held for any
length of time. It is also pertinent to note that laboratory studies
have in all cases been performed on hatchery reared fish and as
Symons (1976) has observed "salmon .... of hatchery stock raised in
slow-flowing water ..... may not have performed as well in fast
flowing water as wild fish would have.".

Drift abundance.

The hypothesis that drift abundance increases with increase in water current velocity was tested by sampling the drift at different current velocities at sites B and C. The results are presented in Fig. 3 and clearly show that this is the case. Drift abundance would be expected to increase with increase in velocity as a consequence of:

1) Increase in the amount of water, containing a fixed concentr--ation of suspended material, passing a fixed point over a period of time.

2) The suspension of material which would remain settled out of the flow at lower velocities.

At site C it appeared that the first effect predominated since the amount of drift increased gradually with increase in velocity. However at site B there was clearly a threshold at about 0.33 m sec^{-1} above which a second phase of material entered into suspension. Inspection of the drift showed that at site C to be composed predominantly of material less than 0.1 cm in diameter, while at site B particulate material was predominantly also in this size range at velocities lower than 0.33 m sec^{-1} while in addition much larger material was present at velocities above this.

Fig. 3. Change in drift abundance with current

velocity.

V   Current velocity m sec^{-1}

W   Dry weight gms

● Site B

○ Site C

NB Drift samples were taken for a duration

of 5 mins at each point, and air dried for

7 days at 20 - 25 degrees C before weighing.

V m/s
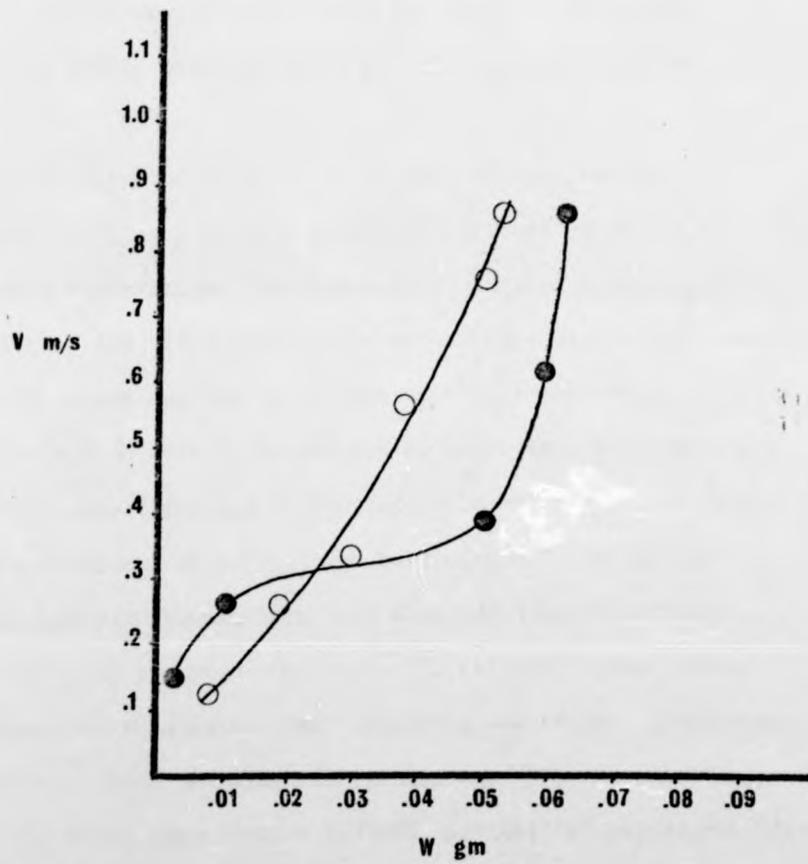
Seasonal and temperature effects.

During the mid-September series of dives, previously densely
occupied sites were found to contain few visible fish, sites A, B, C
and D yielding only 4 to 5 fish between them. These fish, contrary
to previously experienced behaviour, were easily disturbed, fled
immediately and did not return. They did not occupy previously
popular positions. These observations followed a sudden overnight
drop in water temperature from $15^{o}C$ to $7.5^{o}C$ on the 8 September.
Temperatures had slowly risen to $9.0^{o}C$ by the 13th and $10.0^{o}C$ on
the 16th.

Electric-fishing the ridge on which most of the previous
observations had been made at site A was accomplished on the day
following diving observations (16 September). An area extending to
2.0 m each side of the ridge crest and over half the river width was
fished. Twenty salmon and one trout were caught, representing
two-thirds of the fish seen to be stunned as conditions made capture
difficult. This result implies either that fish had moved into this
area since the previous day or had been holding positions, perhaps
closely associated with cover, such that they had escaped detection.

Allen (1941, 3) proposed that below $7^{o}C$ Atlantic salmon became
inactive amongst the substrate. Over-wintering substrate - associated
behaviour has been found in salmonids by Lindroth (1955), Hartman (1963),
Saunders and Gee (1964), Edmundson et al (1968, and Chapman and Bjornn (1969).
Pinder and Eales (1969) have found that Atlantic salmon are less
bouyant in early winter than the rest of the year, which would be
consistent with close association with the substrate. It is proposed
that the apparent absence of fish at the sites at this time of year was
due to their having adopted a shelter-oriented behaviour pattern. The
advantages of remaining amongst cover during the winter would be
1) the avoidance of unprofitable energy expenditure at a time of low
food abundance, 11) prevention of physical damage due to scouring,

111) and the avoidance of predators.

Territorial behaviour.

Territories, in the sense of "defended areas" (Gerking 1953
after Noble 1939), were found to be maintained in some form at all the
sites studied, except at the additional sites a and b (Fig.1 and
Table 1) which will be discussed later. However there was such
variety in the relative extent and shape of such areas and in the degree
of "defence" that it is necessary to consider each site seperately.
Agonistic behaviour will not be described in detail as comprehensive
accounts have been published by Kalleberg (1958), Keenleyside and
Yamamoto (1962), and Jenkins (1969) and the author's own findings
correspond closely. Table 3 lists local fish densities at each site
from which mean territory area can be determined for all sites except
site A.

Logierait (A): On the 29 June four 12.0 cm long fish were
observed foraging individually over the whole area of the leeward
face of the ridge, rarely approaching to within 0.10 to 0.15 m of
each other, and without apparent agonistic interactions. On the
2nd August several 7-8.0 cm fish now occupying the area were seen to
occasionally display to another fish that held a position amongst the
Myriophyllum fronds at the crest of the ridge. No direct aggressive
responses were made. Fish averaging 5 cm in length were observed on
both these occasions. These fish tended to keep away from the upper
slopes of the ridges and were seen to often respond by attack or
submission acts to each other's presence. No display behaviour was
seen.

Exclusive territories were kept by all the fish at this site
only within one body length of the temporary station that the fish
happened to be occupying. The lee slope as a whole acting as a
communal foraging space.

Pooltreight (B): The high current velocity in the lower mid-
water zone (Table 3) on both the 29th June and 2nd August was occupied

by several 12.0 cm fish, foraging over a breadth of about 8 m. Although fish could be seen some 2 m in front of each other only one was seen at any one time to either side. No agonistic encounters were seen to take place, but fish nevertheless maintained these distinctly separate territories and remained above specific areas of substrate in spite of the high current velocity (1.0 m sec^{-1}).

On the 29th of June the substrate at this site was covered with a territorial mosaic (cf Kalleberg (1958) and others) which would appear to be characteristic of fry behaviour in a restricted environment. The fish maintaining these territories were about 4.0 cm in length and held areas 0.3 to 0.4 m wide by 0.5 m long. There was a remarkable consistency in these territorial dimensions from fish to fish. Within each territory fish occupied temporary stations for 10 to 30 secs at a time, working frantically against the current to maintain position on or within 0.02 m of rocks. Fish remained predominantly within their own territories although forays into adjacent territories frequently occured. Trespass into another territory was met by direct aggresive response, but only if the intruder approached within about 0.05 to 0.10 m of the resident's station. By holding many temporary stations over a short period of time fish were able to "patrol" their entire territory.

On the 2nd August there were fewer 0+ fish, now averaging 7 to 8.0 cm in length, occupying larger territories averaging 1.25 to 2.0 m^2 as compared to 0.17 to 0.25 m^2 in June.

Linn of Avon (E): The pool contained a distribution of fish similar to that on the substrate at site B but at much lower densities. Density increased from 0.3 fish m^{-2} to 1.2 m^{-2} along the central axis of the pool from pool head (where water velocity was assessed to be low) to pool tail (where the current velocity had increased 2 or 3 fold). Both 3.0 and 7.0 cm fish moved without apparent undue effort amongst the substrate, remaining closely associated with it although current velocity was relatively low compared to other sites. No agonistic

encounters were seen although fish often came closer than a body
length to each other. The distribution of fish over the substrate was
fairly uniform, implying the operation of a territorial-like
dispersive mechanism.

Girnaig (C): On the 30th June three 8.0 cm salmon maintained
separate irregular territories on the loose rock substrate of the
downstream end of the pool. These fish swam continuously always
remaining 0.05 to 0.10 m above the substrate, never touching any rock
surfaces, possibly making use of deflected currents to maintain
station. These were again temporary stations held for 10 to 20 secs
separated by rapid trans-territory movement. In common with all the
other sites fish were rarely seen to drift downstream (if so then
exclusively head first), usually actively swimming to a new position.
Again agonistic behaviour was only shown if a temporary station was
approached.

A group of 8 to 10 trout and salmon juveniles, 12.0 to 15.0 cm
in length, at the junction of the two streams at the pool head showed
no overt reactions to each others' presence. These fish either swam
vigorously or "rested" (still beating their tails) for up to 30 secs
just above the leeward side of rocks, always facing upstream and
holding one station which was only left to capture food. The area
was densely populated (2-3 fish m^{-2}) and fish often bumped into each
other and this physical contact sometimes resulted in an attempted nip.

Garry (D): Similar behaviour was seen at this site which held
40 to 50 fish of the same size and overall density as at the Girnaig
pool head. It was obvious that these fish found difficulty in
maintaining position in this current. Again fish showed little agonistic
behaviour except that sometimes fish would bump into one another which
often resulted in an aggressive response in the form of an attempted/
successful nip. The "nipped" fish (which was not always the one
responsible for the encounter) moved off and often made contact with

another fish, which might then nip or be nipped. The resulting incident sometimes involved up to 5 fish.

Several points merit further consideration:

There would appear to be a relationship between fish size and territory size within one habitat. At site B fish of 4.0 cm length held territories 0.17 to 0.25 m^2 in area, 8.0 cm fish held ones of 1.25 to 2.00 m^2, and 12.0 cm fish held territories of about 16.0 m^2 in area. This relationship has also been demonstrated by Kalleberg (1958), Stringer and Hoar (1955) and Mason (1969).

At all sites where fish maintained stations within the water flow fish of less than 7.0 cm length (i.e. predominantly 0+) were always closely associated with the substrate, while larger fish remained above it.

Fish of a size less than 5.0 cm were never seen to show display-type agonistic responses. These fish both in fairly static water (i.e. site A) and the highest current velocities in which they were found showed only attack/escape reactions. Larger fish, in the 8.0 cm size range, showed both display and attack/escape responses to each other's presence. All the fish in the 12.0 to 15.0 cm size range were in high velocity currents as a result of which they were highly active and detailed observation of their behaviour proved difficult. It would appear that the incidence of the characteristic territory-maintaining agonistic behaviour was very low in these largest fish, although a well separated distribution was still maintained. Kalleberg (1958) and Hartman (1963) have both observed a reduction in the general level of agonistic encounters at higher current velocities. Kalleberg ascribes this to increased visual isolation caused by closer association with the substrate. Hartman found that such overall decrease was associated in the spring with a great reduction in threat but some increase in direct aggression. This was due almost entirely to the difficulty in maintaining a display

posture at high velocities. He also found that the incidence of
nipping in general increased with water velocity increase. The
possibility that the fish at sites C and D were entering an aggregative
phase associated with the parr-smolt transformation will be considered
in the "Schooling behaviour" section.

At none of these sites were fish of different sizes ever seen
to interact agonistically, except, in the case of transients at site C,
where the occasional upstream passage of large trout elicited abrupt
avoidance and hiding behaviour from resident fish. Symons (1968) has
also noted an absence of agonistic responses between juvenile Atlantic
salmon of different size, and Chiszar et al (1975) found the agonistic
repertories of 0+ and 1+ rainbow trout to be totally different.
Newman (1956), obtained results that "imply that the greatest conflict
may occur between fish of nearly equal size". Unpublished work carried
out by Thorpe on Atlantic salmon juveniles confirms this view.

The lack of territories, other than the immediate area surrounding
the fish, at site A together with extensive use of the ridge lee slopes
as a shared foraging area was a situation very different from that
found at the other sites. The ridge lee was an area of high food
abundance, which together with an absence of any appreciable water
current may have contributed to this behaviour (see following section).

Schooling behaviour.

Fish in high water flow/current velocity drop situations were
found to maintain a social structure whereby they apparently reacted
together as a school rather than as individuals. Such an aggregation,
of 60 to 70 salmon and trout (12.0 to 15.0 cm in length) was found to
occupy a 10 m diameter, 2.0 m deep pool below a 10 m waterfall 0.5 km
downstream of site C on the Girnaig (site c, Fig.1) in June, August
and September. A similar behaviour pattern was found in 6 to 10 fish
(10.0 to 15.0 cm in length) foraging in a pocket of slack water
extending underneath a funnel of water flowing at 4 to 5 m sec^{-1}
(site a, Fig. 1) although this site was only examined on the 13 September.

The low level of territoriality exhibited by fish in the slack
water at site A and the close association between fish of 12.0 to 15.0 cm
length at site D (albeit in a high current velocity) could be regarded
as special cases of schooling behaviour. It is therefore pertinent
to examine possible causes of a departure from territoriality, of
which three can be postulated:

1. Kalleberg (1958) has demonstrated that at current velocities
approaching zero Atlantic salmon fry cease territory-maintaining
behaviour and enter a schooling phase. The implication is that there
is a relationship between water current and territoriality. Fish at
the subsidiary sites a and c were effectively in static-water
environments and a low velocity situation, such as found at site A
may well result in a social structure intermediate between schooling
and territoriality.

2. In situations of rapid current velocity drop (such as found
at site a and A, considerable amounts of suspended material settles
out of the main water flow, resulting in high food abundance
immediately below the velocity drop. There is evidence that high food
abundance acts to reduce the intensity of aggression between competing
resident salmonids, (Keenleyside and Yamamoto 1962, Symons 1968 and 1971,

Slaney and Northcote 1974). Thorpe (1968) has shown that increase in feeding opportunity can result in a decrease in overt aggression between Atlantic salmon fry.

3. The parr-smolt transformation is marked by a change from a territorial to a schooling mode of behaviour (Hoar 1953). Simpson (pers. comm) has shown that changes in the endocrine balance of Atlantic salmon, in particular an increase in thyroid activity, commence during the summer preceding migration. It is possible therefore that fish in the 12.0 to 15.0 cm size class (such as these at sites a, C and D)had already undergone (or were in the process of undergoing) associated modifications of behaviour, resulting in schooling.

Some doubt must be cast, however, on the validity of this third causality. Observations were made on the 14th of September at the subsidiary site b which was on the Tummel about 400 m below the dam at Faskally. Large numbers of 10 to 12 cm salmon were holding stations near or amongst the substrate and sheltering in the lee of rocks and boulders. These fish were all distributed individually over the substrate and did not show any schooling behaviour.

Feeding behaviour.

The results of observations of feeding behaviour are summarised
in Table 6. Both substrate-oriented and drift feeding were observed
to take place. Substrate-oriented feeding was found only in cases where
fish were closely associated with the substrate while drift feeding
predominated at all sites and in all sizes of fish except in the case of
5.0 cm fish at site A. Three distinct types of capture behaviour were
found to comprise drift feeding:

i) Direct capture: A rapid burst of swimming to intercept a
prey item followed by capture and return, almost always, to the original
station. Capture took place above and to the side of the station, and
below in some cases where fish were holding position above the substrate.
In most cases the capture position was upstream of the original station,
although in high current velocity situations (e.g. pool head, site C)
where fish had obvious difficulty in maintaining station it often
took place slightly downstream. Similarly the trajectory usually
appeared to be/straight line from station to capture point, although
again at site C a pronounced S-shaped curve was usually the case, the
fish having to chase the prey downstream to some extent. Prey items were
also chased downstream at site A where fish foraged exclusively facing
downstream to the main current (although this was upstream relative to
the slow ridge lee countercurrent). Material was either captured as it
settled out of the main flow or chased downstream as it was carried over
the fish, the fish dropping out of the main current in order to regain
the lee slopes. These fish were not seen to return to their former
station.

ii) Head jerk feeding: Capture of material passing within 1 or
2 cm of the fish by means of rapid side to side snapping movements of
the head without associated body displacement. This form of feeding
took place in bouts of 10 to 15 secs both while the fish was maintaining
station and during swimming between stations. It was found to be

Site	Fish Age (yrs)	Fish Length (cm)	Current Velocity At Station		Drift Feeding (found at all sites)				Substrate Feeding
			m/sec	bls*	Maximum Capture Distance		Head Jerk	Surface	
					m	bl**			
A	0+	5.0	0.0	0.0	***	***			X
A	1+	12.0	0.70****	6.0****	0.70****	6.0****			X
B	0+	4.0	0.20****	5.0****	0.04	1.0			X
B	1+	12.0	1.00	6.7	0.12	1.0	X		
C	1+	8.0	0.20	2.5	0.20	2-3.0	X		
C	2+	12.0	0.40	3.3	0.30	2-3.0		X	
D	1+/2+	12-15.0	0.90	6.0	0.45	3.0		X	
E	0+	3.0	0.20****	6.7****	0.10	3.0			X
E	1+	7.0	0.30****	4.3****	0.20	3.0			X

NOTES: * body lengths sec^{-1}.
         ** body lengths.
         *** fish showed anormal feeding behaviour - see text.
         **** maximum current velocity fish were exposed to while feeding. The station was held on or amongst substrate and subject to local velocity variations which could not be measured. At site B the figure given was estimated.

peculiar to site B and was exhibited by all sizes of fish.

iii) Surface feeding: The capture of material at the water surface was found to occur at sites C and D only.

The eyes of fish were often seen to swivel and apparently fix some object although only rarely did a capture foray follow. This was especially pronounced in the case of the 4.0 cm fish at site B where capture-at-a-distance feeding occured relatively infrequently: head-jerk and substrate-oriented feeding predominating.

Substrate-oriented feeding consisted either of bouts of foraging on or amongst the substrate or isolated attack and capture sequences involving a particular prey item. During the foraging bouts fish were often seen to attack small algal strands on the surface of rocks, tearing them off, then rejecting them. At site A the 5.0 cm fish appeared to be feeding exclusively on settled drift material which could be seen on the substrate. Fish were rarely seen to reject material after capture except at site E where the overwhelming majority was rejected.

It would appear, from indirect evidence that fish were feeding predominantly on material of very small size. Visual assessment of the drift found it to be composed of relatively fine material at all sites. From laboratory observations it was clear that ingestion of a food item in excess of 20 to 30% of the maximum mouth width involved pronounced jaw and opercular movements. By measurement it was determined that mouth width and fish length were linearly related, fish 4.0 and 12.0 cm in length having gapes of 0.32 and 0.83 cm respectively (chapter 3). As no pronounced ingestion movements were seen it seems likely that even the largest fish were not ingesting prey in excess of 0.17 to 0.25 cm in size. Furthermore, it was impossible to see the prey as it was captured which would not have been the case had the prey been larger.

From Table 6 it would appear that maximum drift capture distances were dependent on the interaction between current velocity and size of

fish, fish of different size at any one site exhibiting similar maxima in terms of body lengths. Bailey et al (1975) observed that pink (Onchorhynchus gorbuscha) and chum (O. keta) salmon fry capture distances decreased with increase in current velocity, the fish remaining stationary in velocities greater than 0.20 m sec^{-1}.

Diel Activity Rhythms.

Observations, using flash photography, on fish maintained in experimental tanks (Chapter 4) showed that these populations developed behaviour patterns anticipating "dusk"and "dawn". After two weeks habituation to a particular photoperiod behaviour changed from current-oriented substrate association immediately preceding the switching-off of the lights to a non-oriented distribution over the entire tank depth one minute after. When the lights were switched-off $1\frac{1}{2}$ hours before the normal time then a similar non-oriented behaviour took 15 to 20 minutes to develop. Similarly photoperiod-habituated fish showed no overt response to the lights coming on at the normal time while lights coming on before this time caused an immediate short-lived panic response. Food input into the tanks was not directly related to photoperiod, commencing 1 hour after "dawn" and ceasing 1 hour before "dusk". No overt behavioural change was related to the food input period although the overall level of activity increased (presumably as a consequence of feeding).

The existence of diel rhythms of activity in salmonids has been well established. Swift (1962 and 1963) found that confined brown trout were diurnal and showed a peak in feeding activity at dawn. Hoar (1942) and Kalleberg (1958) reported a diurnal feeding rhythm, with nocturnal inactivity after a peak at sunset. Recently Eriksson (1977) found activity peaks in Atlantic salmon and brown trout to be closely related to dawn and dusk, although these fish were diurnal only in winter and nocturnal in early autumn and late spring. Ultra-sonic telemetry of the electromyogram of the m. adductor mandibulae of brown trout by Oswald (1977) indicated that there were three daily peaks in feeding activity and that nocturnal feeding was common. Diurnal and nocturnal peaks in feeding activity of trout have also been found by Thorpe (1974), Elliot (1967), Chaston (1969) and Jenkins et al (1970) report a close relationship between stream drift material

occurence and feeding intensity.

The foregoing raises the question of whether juvenile salmonid feeding behaviour is regulated by innate circadian rhythms or whether feeding takes place as the opportunity presents itself (i.e. directly regulated by food abundance). Hoar (1942) demonstrated that feeding can still take place in the total absence of light, and proposed that salmon and trout become habituated to a non-feeding phase during the hours of darkness. Davis and Bardach (1965), as a consequence of a series of laboratory experiments on Killifish (Fundulus heteroclitus) and other species, concluded that "pre-feeding activity is a consequence of conditioning the act of feeding to an endogenous cue which itself is co-ordinated by the time of feeding or daily changes in light." They found that from one to three days were required for the time of pre-feeding activity to shift in response to a shift in lighting or feeding periodicity. The above would seem to indicate that diel rhythms are established with respect to feeding activity but that these are capable of rapid adaptation to changes in prey availability. The observations of feeding and associated behaviour reported by the author began in all cases 4 to 5 hours after sunrise and terminated 4 to 5 hours before sunset. It is therefore likely that feeding behaviour was not studied during the periods when high activity levels would be expected, although the behaviour observed, during the morning and afternoon periods, was therefore more likely to have remained consistent from site to site and day to day, independent of whether peaks at some sites occured at dawn or at dusk.

GENERAL DISCUSSION AND CONCLUDING COMMENTS

It is the purpose of this section to incorporate the foregoing observations of microdistribution and territorial and feeding behaviour into a single conceptual framework. These speculations are based almost entirely on the observations, discussions and conclusions presented in the previous sections and reference should be made to these for supportive evidence. References will be given in cases where (a) additional information (not included elsewhere) is presented, and (b) where further conclusions have been drawn.

The freshwater residence phase of the Atlantic salmon life cycle has long been regarded as purely a feeding and growth stage prior to smoltification and seaward migration. As such the primary function of pre-smolt salmon behaviour must be the acquisition of adequate food and thus an efficient exploitation of the food component of the environment is necessary. Stream and river carrying-capacity is partly dependent on benthic productivity but is also greatly enhanced by the input of material of terrestrial origin (Hasler 1974). Much material is at any one time being passively carried as drift by the current, therefore representing a significant source of food material for stream fishes (Waters 1969). The utilisation of drift prey has several advantages:

    i) Independence of local aquatic and terrestrial productivity.

    ii) Availability of non-aquatic prey material.

    iii) Concentration in certain sharply delimited areas, namely high current velocity and sharp velocity drop situations.

    iv) The hunting/searching component of energy expenditure associated with food acquisition is eliminated if potential prey drifts past the predator (Schoener 1969 and Tuša 1969). Net energy gain per prey item is therefore enhanced.

Juvenile Atlantic salmon microdistribution within the habitats studied was closely related to the maximum locally available current velocity,

fish holding position within or adjacent to this current. Drift
feeding was the predominant method of food acquisition, although
foraging on substrate-associated prey occured where position was
held on or amongst the substrate. It was not clear whether substrate-
oriented feeding was on benthic-living organisms or on material which
has settled from the drift. Two discrete behaviour patterns
comprised drift feeding. Head-jerk capture (page28) was used to
feed, apparently indiscriminately, on material passing close to the
fish. Swimming and capture forays, involving location of a particular
drifting prey item and its subsequent capture, were more common and
extended the feeding range to a distance of several fish body lengths
from the position being held (pages 28,29). The maximum capture
distance was linearly related to fish length implying a close relation-
ship with swimming ability (Bainbridge 1958).

A fish size-dependent swimming ability was also responsible for
segregation of different size groups into effectively different
microhabitats. Larger fish maintained position in faster currents,
thus fulfilling to some extent their increased food requirements which
would otherwise have been expressed as feeding spaces of potentially
unmanageable size (see p. 21). The food requirements (amount,
particle size etc.) of different size groups are essentially
different, thus permitting co-existence at one site (page 25)(this
situation is essentially similar to that of closely-related sympatric
species, MacArthur (1972)). Within one size-group these requirements
are potentially identical hence the necessity of some mechanisms to
assure adequate sharing of this resource. In Atlantic salmon food
resource sharing operates through a formalised (i.e. "contest-type"
as opposed to "scramble" competition) mechanism of feeding space
partitioning. This is accomplished through agonistic interactions
between the individuals concerned, resulting in the maintenance of
individual feeding territories. The intensity of aggression

increased as the size difference between individuals decreased
(page 21), thus assuring the efficient use of energy associated with
territory maintenance. This situation is essentially analogous to
that of closely-related sympatric species, although in this case
character-displacement is usually the operative mechanism (MacArthur
1972).

Territory represents a fundamentally three dimensional
exclusive feeding space. The intensity of aggression was maximal in
the immediate vicinity of the station being occupied and decreased
rapidly with distance. Thus only a small space could be actively
defended at any one time. A similar limitation existed on the
extent of the feeding space available at any one moment without
movement to another feeding position. Total feeding space size, in
any one habitat, increased exponentially with fish size (page 24) and
Allen (1969) while/immediately accessible from one station increased
                       that
linearly. Thus in habitats where prey abundance is such that
sufficient food cannot be obtained by predation based from one station
several temporary stations are held, the frequent use of which ensures
maintenance of the total territory.

The relationship between interindividual aggression, territory,
feeding space and total space or area within which the fish foraged
over a period of time was complex and variable:

i) Fish maintained school-type social structure, feeding
together as a group without individual territoriality, possibly
a communal territory coinciding with the foraging space.
This behaviour was found only in the case of the 12 to 15 cm
size class in static water habitats.

ii) Intense aggression limited to the space in the immediate
vicinity of fish feeding individually over an extensive
shared foraging space which may have represented a
communally defended territory. All size classes of fish

exhibited this form of organisation but only when current velocity was very low at stations held adjacent to a sudden current velocity drop.

iii) Intense aggression limited to the immediate vicinity of the station, from which fish fed individually, although an individual territory (maintained by frequent use of several temporary stations) coincided with the foraging space, thereby assuring its exclusivity. This form represents the "classical" territory described by Kalleberg and others, and was characteristic of all size classes of fish in some high current velocity situations.

iv) Aggressive responses limited to reaction to physical contact (but whether within a heirarchic social structure or due to repressed territorial aggression is not clear), dispersion being such that fish fed individually within each exclusive feeding space (which may have represented a territory). This behaviour was shown only by fish of the 12.0 to 15.0 cm size class in some high current velocity habitats. It is possible that this behaviour pattern represents a special case of that described in i).

It is likely that these forms of behaviour represent discrete points along a gradient from intense territoriality, through neutral response, to a rigid hierarchic-type social structure (Baerends and Baerends van Roon 1950). As aggression is closely related to feeding it is further proposed that the above behavioural patterns are related to prey availability, responses to which are modified by water current velocity and fish size.

CHAPTER 2.

The Visual Basis of Feeding Behaviour.

Contents:

INTRODUCTION

Predator Response to Prey.

Predation, the process by means of which an animal acquires
food is the main interface between predator and prey populations.
The total number of prey eliminated by the predators is the product of
the number of predators and the number of prey killed by each predator.
Thus the mechanism of prey consumption by the predator is of
fundamental importance in understanding predator - prey interactions.
The responses of the predator-prey system to prey consumption by
individual predators can be divided into a number of components each
of which can be expressed in formalised terms and their interrelation-
ships defined by the construction of mathematical models (e.g. Lotka
1923, Volterra 1931, Nicholson and Bailey 1935, Gause 1934, Watt 1959,
and Holling 1966). The major criticism of almost all these models is
the simplicity of their theoretical assumptions, and the resultant
poor approximation to reality. Nevertheless they offer an extremely
useful bridge between the study of the behaviour of an animal and its
integration with the animals' ecology. This is especially true in the
case of predation where behaviour cannot be meaningfully interpreted
in isolation.

Holling (1966) proposed a model that is perhaps the most useful
in that its repreٌentation of reality is based on experiment rather than
theory. In general it is a development of earlier models and states
that at any one prey density the number of prey attacked by one predator
depends only on the predators' rate of successful search, the time
prey are exposed to the predator, and the time spent handling each
prey. The period of time prey are exposed to salmon juveniles has
been given some consideration in Chapter 1, and considerations of
handling time are examined in Chapter 3 as they are directly related to
the mechanism of feeding. The rate of successful search can be divided
into four sub-components (adapted from Holling 1966):

Predator velocity

Prey Velocity

Predator awareness, reaction and strike distances

Capture success.

Since the prey of juvenile Atlantic salmon drifts passively in the water current and the predator actively maintains position against that current the immediate environment of the predator, containing the prey, is in fact stationary relative to the predator which therefore swims at a velocity "x" through it. Thus the prey velocity is zero and, in a constant flow, we can consider the predator velocity to be a constant. Since it is the difference between these velocities that in part determines predator success, it follows that under these conditions predator and prey velocities can be eliminated as variables affecting the rate of successful search. Variation in current velocity, hence the predator velocity if it is to maintain position, will affect only the distance at which the predator can capture prey - the striking distance.

Before discussing the remaining variable sub-components consideration must be given to the mechanism of prey location and recognition. Juvenile salmon and trout of all species are "visual predators". This has become overwhelmingly clear both from the authors own observations (Ch.1) and published material (Polyak 1957, Ali 1959, Protasov 1968 and Ware 1973). Although prey capture may take place below the retinal rod threshold (Hoar 1942, Ali 1959 and Chapter 1) there is no evidence that this implies an alternative prey location mechanism other than chance encounter.

Awareness Distance:

This is the maximum distance at which the predator can see the prey. More precisely it should be represented as a space whose shape will depend on the predators' visual mechanics, in terms of visual fields and zones of enhanced acuity. The distance of awareness will

depend on the contrast between the prey item and background. Contrast is a complex function of absolute prey size, relative brightness of prey and background, and the optical properties of the transmitting medium. The distance of awareness (r_a) has been described by Holling (1966) in terms of the minimum visual angle ($\underline{a}$, the angle subtended at the eye; a measure of acuity) and the length of the prey (L) for a visual predator IN AIR:

$$r_a = L \ / \ \tan \underline{a}$$

However contrast also depends on the relative brightness of prey and its background which is a function of their respective spectral distributions. Thus r_a will vary depending on the particular prey/background colour combination. A further complication introduced where water is the transmitting medium is the high level of light attenuation in comparison with air in which attenuation can be regarded as negligible. Attenuation is very strongly wavelength-dependent, even in clear or distilled water (p.53). Thus in water the awareness distance will depend on:

Prey length

Predator visual acuity

Prey and background colour (i.e. inherent contrast)

Light attenuation (which varies with the amount of dissolved and suspended material).

Reaction Distance:

It can be assumed that an animal will react in some positive or negative way only to an object which, or the effect of which, it recognises. Thus a pre-requisite of reaction must be the resolution of an object so that some physical characteristic is recognisable; mere awareness of its presence in the field of view is not enough.

Striking Distance:

Recognition of an object immediately involves a decision as to the action, if any, to be taken. Thus on location of a suitable prey

item the predator has two choices: to strike (or pursue) or to search again. Since both choices result in the animal being ready to start a new search the better decision is the one likely to yield more per unit time, i.e. "an animal should elect to pursue an item if, and only if, during the time the pursuit would take place it could not expect to locate and to catch a better item" (MacArthur 1972). A further limitation is that there should be a net energy gain to the consumer as a result of the strike. This clearly places limitations both on the striking distance and on the minimum prey size (weight). These variables are interlinked as an increase in prey size (gross energy gain) would compensate for an increased striking distance (gross energy expenditure).

Capture Success:

The overall success of capture is dependent on recognition success and the correctness of the decision to strike. Recognition success depends on familiarity, and clearly the more precise the recognition the less the likelihood of an uneconomic decision to strike. Other factors likely to influence the decision have already been considered, although in addition to these an appreciation (through experience or otherwise) of the local environment likely to affect the strike will be necessary to avoid impossible attempts.

There is evidence that some teleost fish develop a search image similar to that found in mammals and birds: Ivlev (1961) found that prey selectively depended strongly on previous training. Of particular significance are the results of experiments conducted by Bryan and Larkin (1972) who found that individual rainbow and cutthroat trout showed preferences that led to persistent specialisation by individuals.

Prey Characteristics.

A prey item has four characteristics by means of which its visual appearance can be completely defined: colour, size, shape and behaviour.

The colour of an object, to a large extent irrespective of its size, affects its visibility in water and is thus in part responsible for determining predator awareness and reaction distances. It will therefore directly affect the probability of capture and can be of obvious advantage to the prey, for example in the case of camouflage colouration. Zaret (1972) found that the intensity of predation by Melanaris chagris on different morphs of Ceriodaphnia cornuta depended only on the area of eye pigmentation, as otherwise the cladocerans were relatively transparent. The recognition of a prey item by its colour appears to depend on previous experience. Protasov (1968) has shown a relationship between natural diet and colour preferences in several teleost fish and Labas (1959) reports that prey colour preferences of salmon and trout depended on previous feeding experience. Experimentally, problems arise with attenuation of some light wavelengths in water so that the colour in air may bear no relationship to that in water. It is likely, anyway, that in the case of a visual feeding animal where recognition takes place at a distance that relative contrast, rather than colour per se, would be the important variable. Rainbow trout have been shown (Ginetz and Larkin 1973) to have preferences for particular colours in particular backgrounds settings, the order of preference reflecting a direct relationship with contrast.

Prey size to a large extent determines awareness distance, directly affects recognition and reaction distances, and determines the economics of the strike. Size has long been considered of fundamental importance in predator-prey interactions and much experimental work, reviewed elsewhere in this Thesis, has been published on this subject.

The shape of an object may have a twofold effect. It may affect visibility, for example a diffuse shape would be harder to detect against a complex background than a compact shape, and secondly recognition is likely to depend on familiarity with certain shapes. Boulet (1960) found that perch (Perca fluviatilis) showed no preferences for particular shapes, and Protasov (1968), working on a variety of teleost fish, reports species-specific behaviour, some species showing no preferences, others a strong preference for simple shapes, complex shapes, or shapes simulating natural prey organisms. The apparent shape(and size) of natural prey can of course be altered by a suitable pattern of colouration.

Probably the most difficult aspect of a prey item to define precisely with respect to its effect on predation is its behaviour. Behaviour likely to affect the overall availability of prey can be divided into certain categories, namely: concealment, motility, escape reactions, and resistance to swallowing. Neill (1938) found that differences between the frequency of specific items in brown trout stomach contents and their frequency in the environment could be explained almost entirely by the application of a correction based on the degree of exposure resulting directly from the habits of the prey. Similarly Allen (1941) and Ivlev (1961) showed that prey selection depended on its accessibility. Moore and Moore (1976), working on the flounder (Platichthes flesus) found that prey motility and escape reactions had a pronounced effect on capture success. Hartman (1958) found that the maximum size of trout fry ingested by a given size of rainbow trout was greater than the maximum size of Trichopteran or Plecopteran larvae which could be ingested. Observations showed that this was due to the trout finding great difficulty in swallowing the latter two types of prey, which attached themselves to snout or jaw, often pulling themselves free.

From an experimental point of view prey behaviour and shape

variations are difficult to define in a way meaningful to their effects
on predator-prey interactions, and the precise role of prey colour
per se is difficult to interpret. Furthermore predator responses to these
characteristics are confused with preconditioning and individual
preferences.

The experiments reported in this chapter are concerned with reaction
and striking fields. Atlantic salmon juveniles maintain position and
feed on whole drifting prey in the water current (Ch. 1). A simplified
simulation of these conditions was provided by means of a recirculating
flume tank within which feeding activities took place and were recorded.
Simple prey were used of which the shape and colour (near-spherical and
dark red respectively) were uniform, and behavioural movement was absent[*].
The effect of size variation was investigated as this characteristic can
be most precisely defined. Problems associated with pre-conditioning were
minimised by feeding a wide range of prey sizes to the stock fish and
enforcing a long period of food deprivation prior to the experiments. In
order to avoid complex experimental apparatus and data handling problems
the reaction and strike fields were recorded as two-dimensional areas
in the horizontal plane. It is appreciated that these fish feed in a
three-dimensional environment and observations reported in Chapter 1
confirm their use of a feeding space (as opposed to area). Consequently
the design of the apparatus was such as to reduce scope for prey and
predator movement in the vertical plane, thereby avoiding potential
recording inaccuracies.

The salmonid eye, its visual mechanics and properties are
described and discussed following the results of the experiments
outlined above. An analysis of head orientation during the strike and
eye movements preceding and during capture is also presented.
Reference is made as far as possible to the salmonid visual system, but

[*] Drifting prey behavioural movement is unlikely to represent a significant
component of total movement, the major component of which is imparted
by the water current (Cf current velocity measurements, Chapter 1).

as the majority of published work has been done on other teleosts some inferences may be drawn from other species.

Results are discussed only within the context of awareness, reaction, and strike fields and further aspects of the responses of salmon juveniles to prey are considered in Chapter 3.

EXPERIMENTAL MATERIAL.

Predator.

Eggs were obtained from known pairings of Atlantic salmon, and maintained at the Department of Agriculture and Fisheries for Scotland (D.A.F.S.) experimental smolt rearing station hatchery at Almondbank, Perthshire. Pre-feeding alevins were transferred to rearing tanks at the D.A.F.S. Freshwater Fisheries Laboratory at Faskally, Perthshire. These tanks were circular, two metres in diameter and of the radial flow/peripheral drains type extensively used as stock rearing tanks by the Department (D.A.F.S. Report for 1970, 1971), and described by Minaur (1973) and Petit (1973). Stock fish were maintained at ambient water temperatures and fed on a diet of Ewos salmon feed (Astra-Ewos AB, Sweden) in accordance with the manufacturer's recommendations.

The origin and environmental history of each fish was thus known. All fish used for each experiment were of the same stock and kept together under the same conditions. Fish used between the 8th and 28th of June were the 1+ progeny of a single cross, 11th to 14th August and 21st to 28th September fish were 0+ and similarly from one cross.

Prey.

Crumbled Ewos salmon feed was used as the prey. This was sieved using a set of close-tolerance Test Sieves (Endecott's London) into discrete, limited range, sizes. The optimum size was determined in the growth experiments reported in Chapter 4 and was that giving maximum growth over the period of time studied for a particular size of fish.

METHODS

THE FLUME TANK

The flume tank was constructed to give an experimental area of one metre^2. Recirculation was accomplished by means of an electric 7.5 H.P. 6 inch/728 Selfline Pump (Holden and Brook Ltd., Manchester) which was an impeller-type pump with a maximum capacity of 45 litres sec^{-1}. It was installed in line with a simple system of 6 inch (15.24 cm) nominal bore (n.b.) rigid PVC (Durapipe) piping (Fig.1). In practice the maximum flow could not be achieved due to the formation of a standing wave oscillation within the main return pipe (1). The resulting unstable pressure differential between the inlet and outlet sides of the pump caused surges of water flow. To avoid this effect and provide control over the water flow volume, a 4 inch (10.16 cm) n.b. crosspipe and ball valve (2) was fitted to connect the upstream and downstream sides of the pump thus acting to equalise the pressure differential. The system could not be run with the ball valve closed and standard positions of valve opening were selected. These were: fully open, three quarters, one half and one quarter open, flow volume (and therefore current velocity at a particular water depth) increasing in that order.

The whole system could be drained by means of a valve (3), complete drainage being facilitated by the flume outlet being flush with the flume bottom (4). The flume itself was isolated from pump vibrations by a neoprene rubber bellows flexible joint (Engineering Appliances Ltd., London) between the pump and flume (5), and by mounting the heavy reinforced concrete pump base on a sheet of high density rubber.

The flume tank (Fig.2) was constructed of 1.5 cm thick plywood painted with waterproof synthetic paint of a light pink/grey colour and all the joints were sealed with a silicone rubber sealant/adhesive. One side was fitted with a 0.64 cm thick plate glass window. Reinforcement

Fig. 1   Recirculation Pipework.

1. Main return pipe

2. Cross pipe and ball valve

3. Drain valve

4. Flume tank outlet

5. Neoprene rubber flexible joint

6. Flume tank inlet

7. Pump

8. Plate glass window in concrete tank

9. Concrete tank walls

10. Concrete tank base.

PLAN VIEW

SIDE VIEW

0   m   1·0

PLAN VIEW

SIDE VIEW
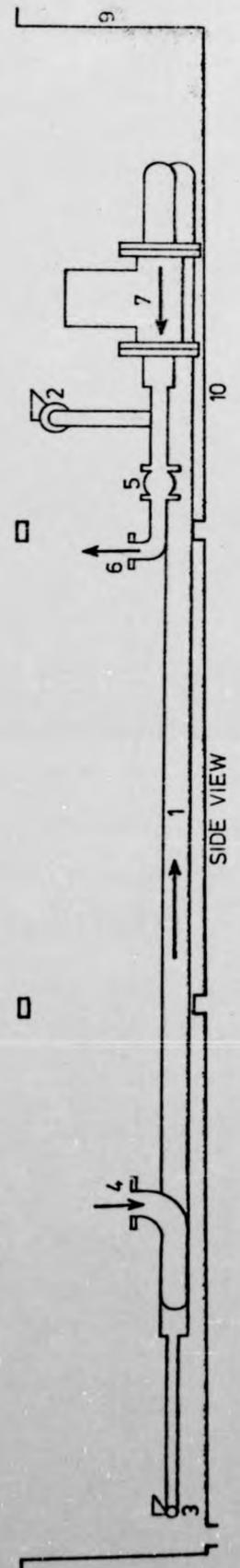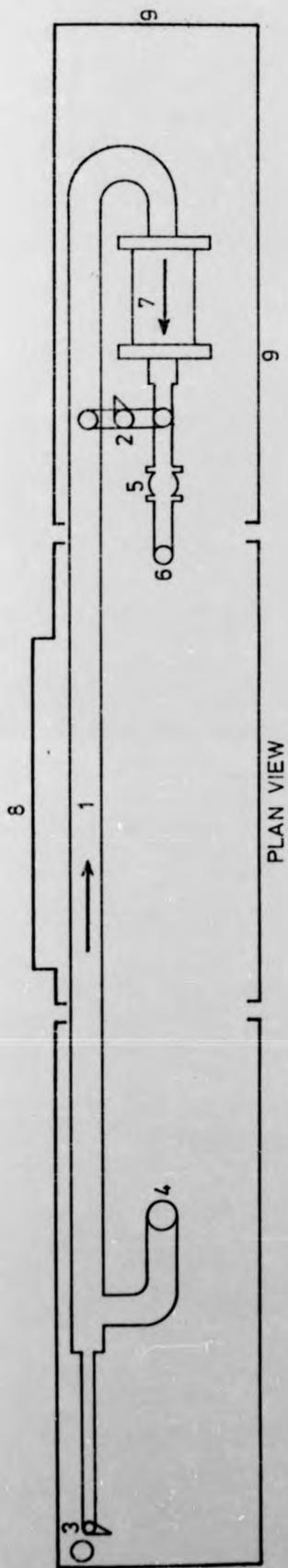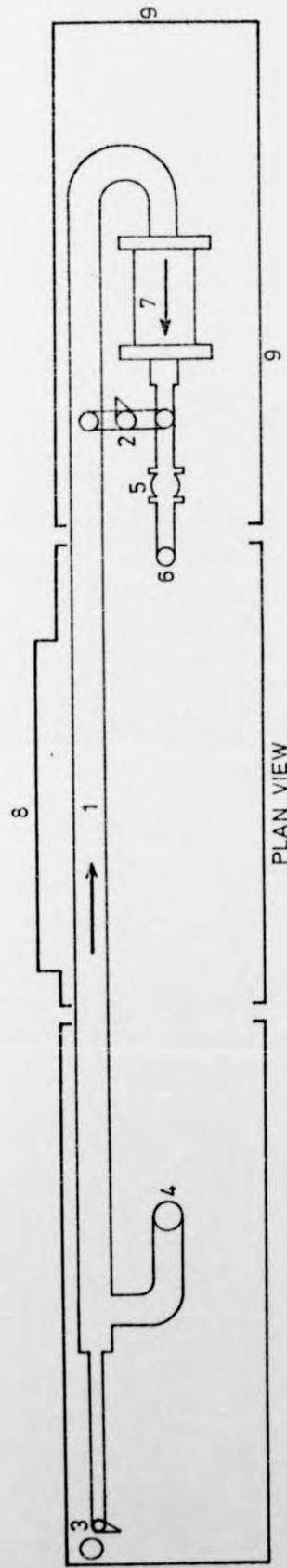
0   m   1·0

Fig. 2   The Flume tank

1. 4" nb inlet

2. 6" nb outlet

3. Stainless steel hemispherical deflector shield

4. Aluminium alloy tank floor

5. Plate glass observation window

6. Plate glass window in concrete tank

7. Adjustable height ballcock water inlet (from filter)

8. Outlet cover plate

9. 2" nb standpipe and joint (allowing height adjustment)

10. Drain in concrete tank

11. Concrete tank walls

12. Concrete tank base

13. Experimental area

14. Holding area

15. Splash guard.

A - F. Baffles.

Ⓐ Ⓑ   Velocity profiles.

PLAN VIEW

LATERAL SECTION
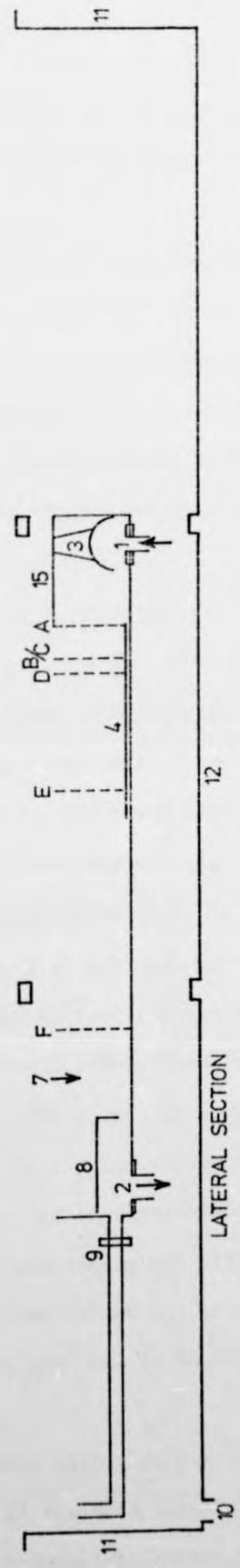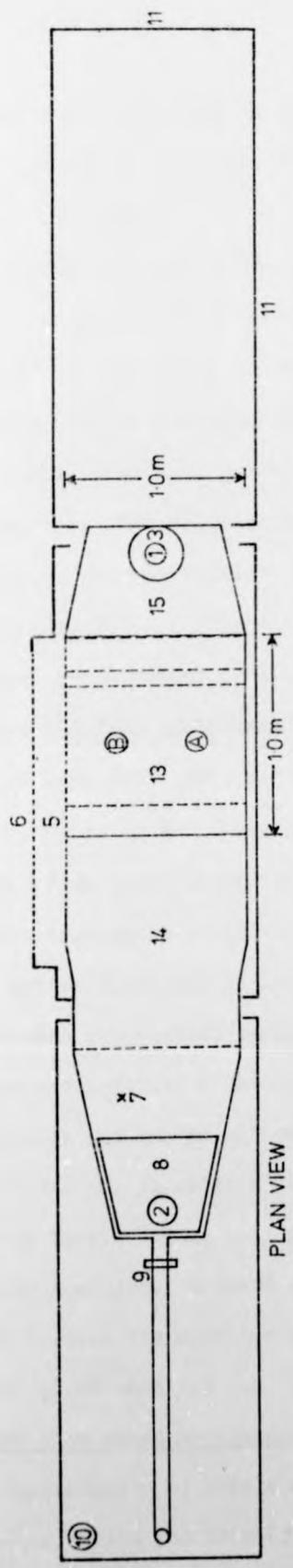
was provided where necessary on the outside of the tank and the whole
mounted on a stand to clear the recirculation piping. Dimensions are
indicated in the figure.

The tank bottom within the experimental area was covered in 0.64 cm
thick aluminium sheet. This provided a reflective surface for photographic
purposes and location for a series of adjustable vertically-placed baffles.
These baffles (Fig 3) consisted of a welded stainless steel frame on
which woven stainless steel wire mesh (aperture size as indicated in the
fig.) was mounted. The upstream baffles (3,A-D) smoothed the water flow
characteristics and were fitted where indicated with nylon monofilament
Grit-gauze ("Nybolt" John Stanair & Co., Manchester). The middle baffle
(E) separated experimental from holding areas while the downstream one
(F) retained the fish in the holding area. The upstream and middle
baffles were adjustable fore and aft and were held in position by pins
fitting into holes in the flume aluminium floor and along the top of
side walls. Fish could be transferred from the holding to the experimental
area without netting by using the connecting hatch (13).

The entire flume and recirculating system was mounted in a slightly
larger concrete observation tank. This allowed for the rigid attachment
of fittings and provided a massive vibration-free base for mounting
feed dispensers and camera equipment. The flume was positioned such
that its window was opposite a large observation window in the wall of
the concrete tank. Beyond this window was an observation and control
room for the operator. A sheet of Solarshield glass (Pilkington Glass Ltd),
was fitted between the operator and flume window and acted as one-way
observation glass when the observation room was in darkness.

Water flow characteristics.

By manipulation of baffle aperture sizes, relative baffle spacing
and deflector shield position (3 Fig 2) the best possible water flow
characteristics were obtained. Highly turbulent water, imparted with
a helical flow pattern by the pump impeller, entered the flume and its

Fig. 3 Top, transverse section through flume tank, showing

arrangement of upstream baffles. Experimental

area is at centre.

Bottom, end on view of single baffle, showing construction

and location in tank.

1. Splash screen

2. Direction of water flow

3. Water surface, set at 22.0 cm depth

4. Flume tank base

5. Aluminium bottom

6. Baffle, diminishing surface waves

7. Feed dispenser outlet tube

8. Extent of serial holes in aluminium base and flume tank side
   walls, to enable fore and aft movement of baffles.

9. Location pegs of baffle frame, within corresponding holes in
   tank bottom.

10. Stainless steel baffle frame

11. Locating pegs and holes on flume tank side walls

12. Baffle mesh:-

    A   5mm aperture size

    B   5mm aperture size fitted with 236 micron Nybolt

    C   5mm aperture size fitted with 475 micron Nybolt

    D   2mm aperture size

    E   5mm aperture size

    F(Fig 2) 5mm aperture size

13. Hatchway, baffle E only.

        ⌐ Removable to facilitate cleaning ¬
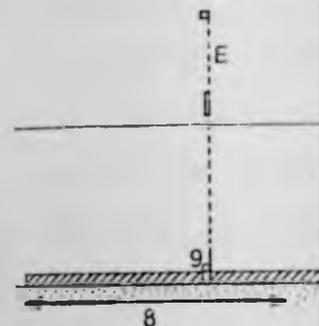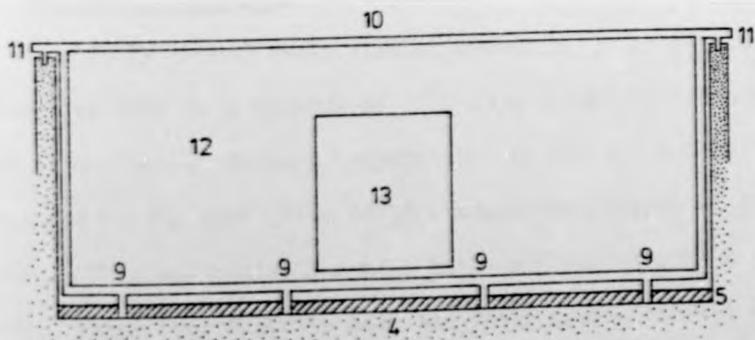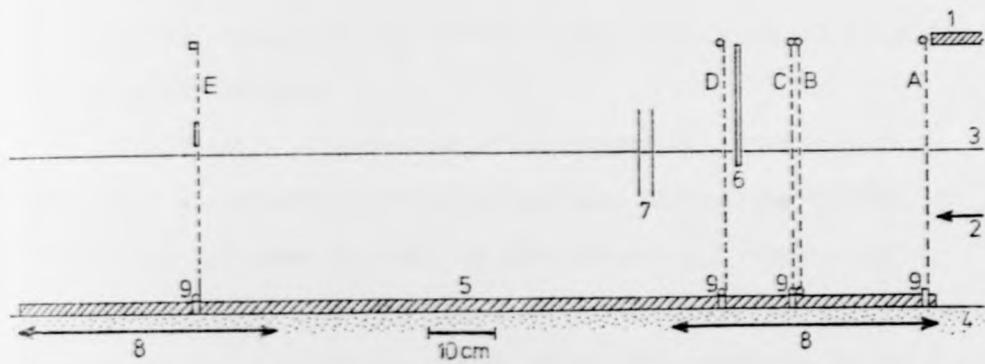
flow was broken up by the deflector shield. Passage through the baffle series eliminated all turbulence and imparted a near rectilinear flow. These baffles, and also the cover plate over the outlet which prevented the formation of a suction vortex, eliminated all but a few suspended air bubbles.

Figs 4 and 5 show vertical velocity profiles taken through the water flow at different ball valve openings. A Kent-Lea Miniflo 265-3 probe and meter was used, checked against a Norvar Streamflo system. As can be seen from fig. 6 these velocity patterns split into two groups, fully and $\frac{3}{4}$ open giving similar flow patterns, as did $\frac{1}{2}$ and $\frac{1}{4}$ open. With increase in flow volume the pattern became less rectilinear, the biggest effect being a surface layer velocity reduction. This was found to be due almost entirely to the effect of feed dispenser tubes projecting 7.5 cm, and also a solid baffle projecting 2 cm below the water surface (fitted to eliminate surface ripple effects). Both these fittings were mounted to the feed dispenser frame described in the following sections. Throughout the depth of water in which feeding took place (i.e. the lower half of the depth) near-rectilinearity was maintained.

Temperature control.

On a fully closed recirculating system water temperatures increased rapidly to a maximum of $45^{\circ}C$ as a result of the heating effect of the pump. To keep temperatures within the normal range experienced by the fish (1 to $22^{\circ}C$) a small throughflow of fresh water was used. This was controlled by a ball-cock and standpipe arrangement (Fig 2). Water from Faskally Loch was first passed through a cylindrical filter housing 1.5 m long by 0.25 m diameter filled with a filter medium of 6.7 to 9.0 mm diameter expanded polystyrene beads. Both the ball-cock and standpipe were adjustable to control the volume of throughflow and water depth in the flume. A throughflow of 0.5 litres sec^{-1} normally proved adequate depending on incoming water

FIG. 4   Vertical Velocity Profiles, ball-valve ¾ open

FIG. 5   Vertical Velocity Profiles, ball-valve ½ open

    1. Profile below feed dispensers
    2. Profile mid-way between feed dispensers and rear
        baffle
    3. Profile 2 cm upstream of rear baffle

In all cases observation window is on right hand side of profile
Velocity contours at 2 cm sec^{-1}. intervals.
Profiles taken at right-angles to flow direction.

4.1

4.2

4.3

5.1

5.2

5.3
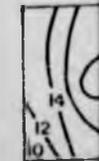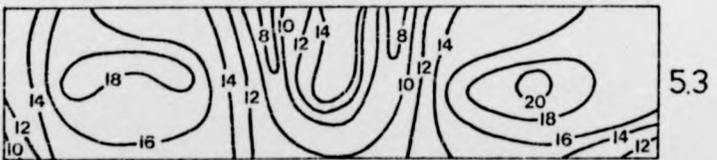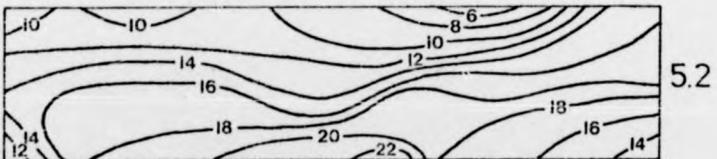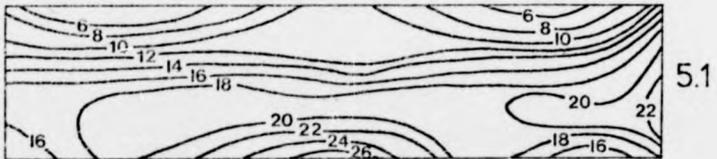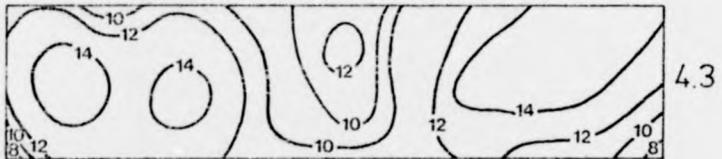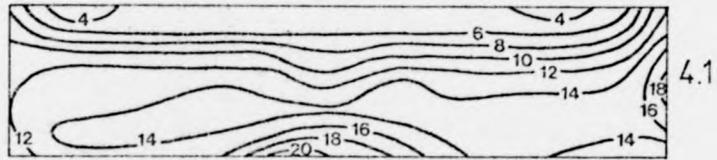
Fig 6. Vertical current profiles, mid-way between feed
dispensers and rear baffles.

Top - 33 cm in towards centre of flume from outside
wall ((A), Fig 2).

Bottom - 33 cm in towards centre of flume from observation
window ((B), Fig 2).

Ball valve fully open ·····

Ball valve $\frac{3}{4}$ open ----

Ball valve $\frac{1}{2}$ open ---

Ball valve $\frac{1}{4}$ open ——
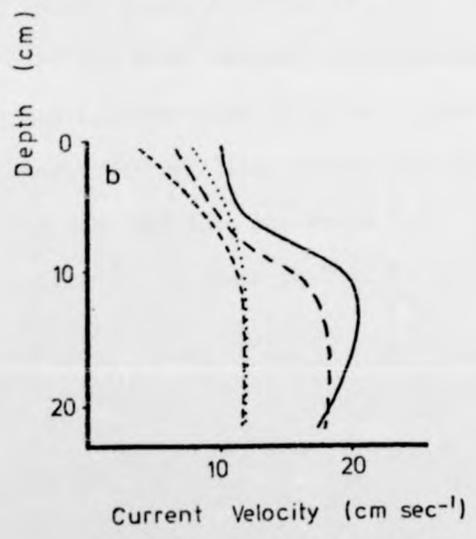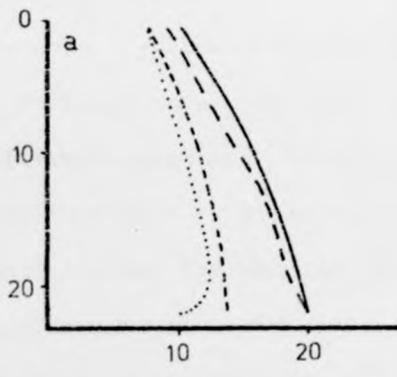
temperatures. This was equivalent to a throughflow of the total flume + piping volume every 30 mins. Recirculating water temperatures were always 2 or 3 degrees C above that of the incoming water.

Feed dispensers.

A series of 23 equally-spaced individually operated feed particle dispensers were mounted on a frame fixed to the external concrete tank. Fig. 7 shows the structure and positioning of the frame and the construction of a feed dispenser. The frame allowed the height of dispensers and other attached equipment to be adjusted. Individual dispensers were actuated by depression of the appropriate actuating syringe (9) in the observation room. The resultant compression of air in the connecting tube displaced the dispenser piston thereby ejecting a food particle placed in the dispenser cylinder (11). By using partially submerged guide tubes (14) the feed particle could be contained beneath the dispenser until it had absorbed some water and surface-adhering air bubbles were displaced. The resulting barely negatively bouyant particles sank out of the tube and into the water flow. A characteristic trajectory within the water flow is shown in Fig. 8.

Fig 7 Feed dispenser design.

Top - end view of frame in position in flume tank

Bottom-lateral view of one feed dispenser and associated structures.

1. Attachment beams, located in side walls of concrete tank.

2. Cross-beam.

3. Vertical members of feed dispenser frame.

4. Horizontal member of feed dispenser frame.

5. Feed dispenser cylinders (23 in total).

6. Water surface (depth set at 22.0 cm).

7. Side walls of flume tank.

8. Direction of water flow.

9. 20 ml actuating syringe.

10. 3 mm i.d. polyethylene tubing.

11. Dispensing cylinder and piston.

12. Food particle position.

13. Aluminium stop-plate.

14. Glass guide tube, 1cm i.d., 18 cm long.

15. Baffle screen "D".

16. Splash screen.
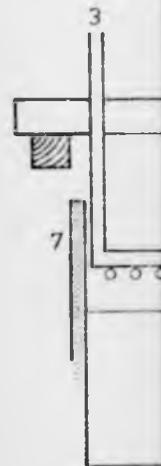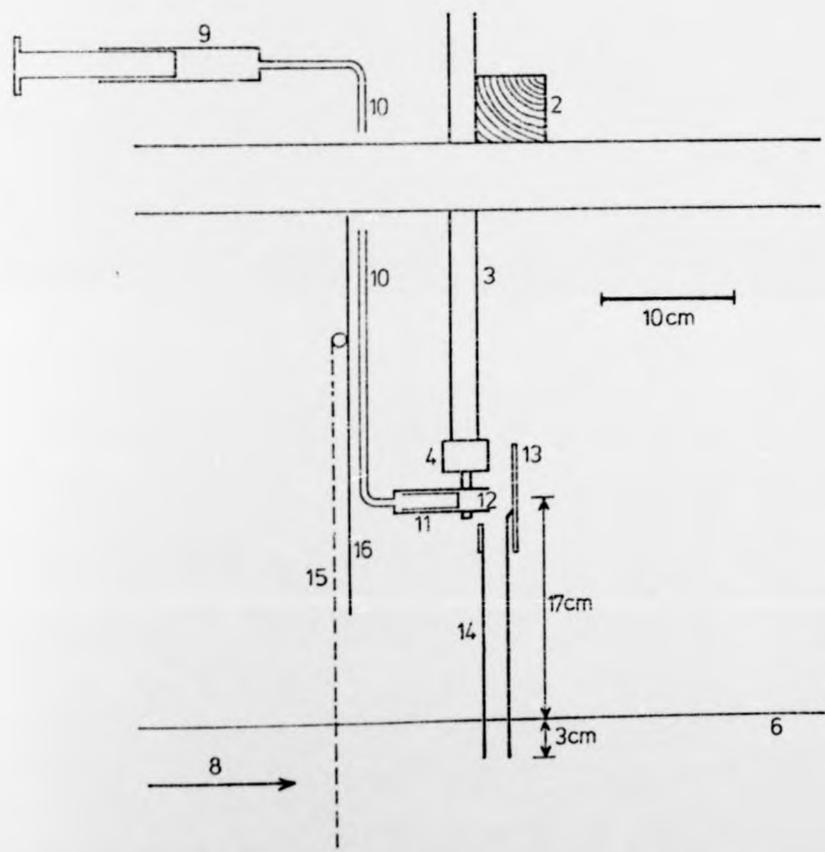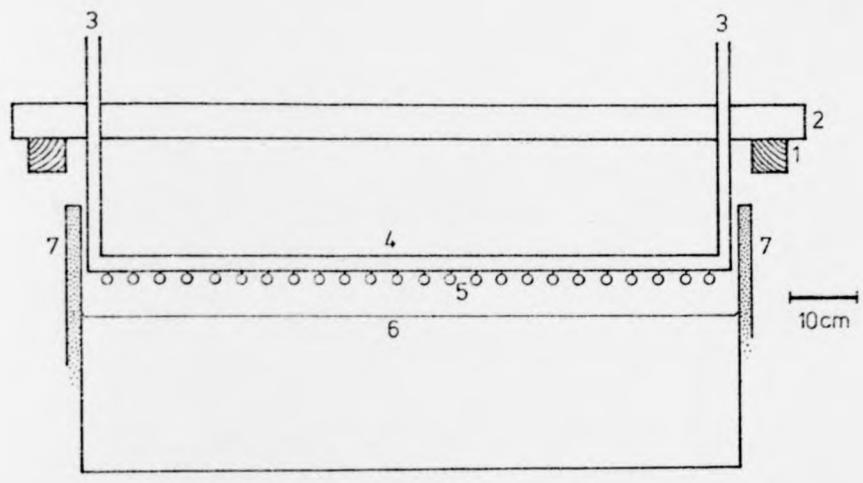
Fig 8 Typical food particle trajectory.

Top Plan view

Bottom Lateral view.

WATER FLOW

BAFFLE D

WATER FLOW
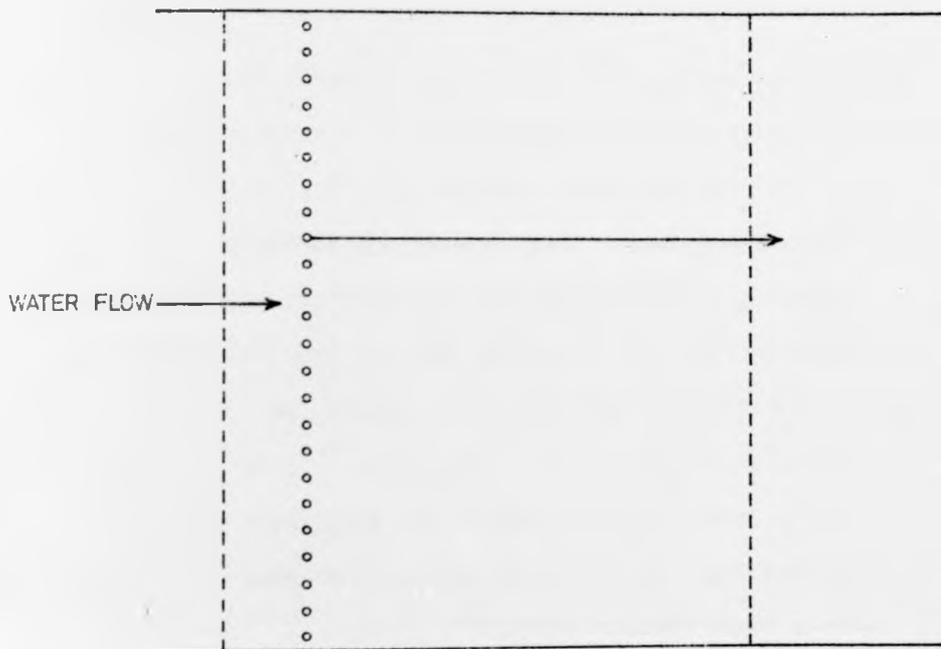
WATER FLOW →

BAFFLE D

FOOD DISPENSERS

BAFFLE E
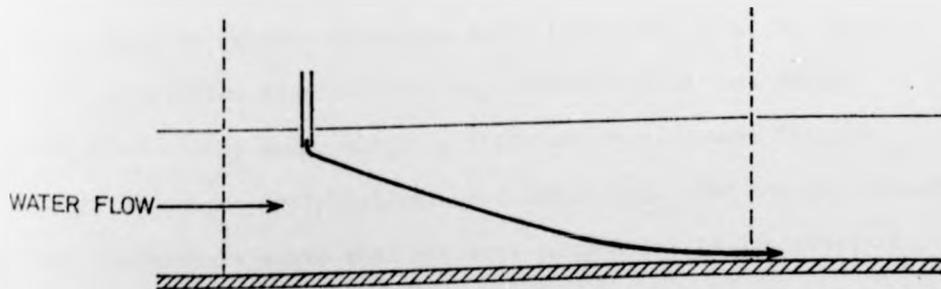
WATER FLOW →

ILLUMINATION

Problems associated with illumination of the experimental area
were twofold:

1) Provision of light of an intensity and spectral composition
within the range under which salmon juveniles normally feed.

11) Provision of light of a suitable intensity to permit high
resolution photography during which the elimination of
water surface interference effects was also a priority.

Salmon juveniles were observed to feed in the wild on both very
sunny and dull rainy days representing a surface light intensity range
in the order of 10^1 to 10^{-1} Watts per m^2 (Wm^{-2}) (10^4 to 10^2 Lux.)

A preliminary experiment was conducted using a small clear
acrylic sheet flume tank to determine the effect of light intensity
on feeding behaviour. Incandescent tungsten filament light sources
were used as these emit a broad spectrum and when run at temperatures
approaching $3,000^{o}C$ wavelengths between 300 and 800 nm are well
represented. Ali (1961) has found the visible spectrum of Atlantic
salmon to range from 364 to 690 nm. A range of source powers from
5 to 250 Watts was used, adjusted using a solid-state dimmer device
to filament temperatures within the range of 2,500 to $3,000^{o}C$, as
measured using an optical micro-pyrometer (Pyro-Wark GMBH, Hanover).
Spectral composition does not vary appreciably within this range
(De Vos 1954) and by using slightly different temperatures in each
case light intensity manipulations were simplified. The use of a standard
filament temperature means that spectral composition is the same, at
this temperature, irrespective of intensity which is governed by
source wattage.

Feeding behaviour on suspended pelleted feed was examined within
the range 9.69×10^{-3} to 9.69×10^1 Wm^{-2}. Water temperature were
maintained at 17.5 ($\pm$ 0.5)^{o}C and 45 minutes was allowed for fish to

adapt to each intensity (Ali, Stevenson & Press 1961 and Ali 1962).
One hundred and eighty four trials on fish were undertaken. No
difference was found in reaction and acceptance/rejection patterns
between light intensities.

Flume tank illumination and photographic recording equipment
was consequently designed to function within the mid-range of these
intensities. "Warm-daylight" fluorescent tubes were used due to their
inherent high efficiency and source uniformity with time and over the
area under illumination.

Photography was accomplished from above the flume by mounting the
camera system on a heavy frame clamped to the concrete tank directly
above the centre of the experimental area (Fig 9). The lighting
system was mounted either side of the camera. This resulted in severe
water surface reflections which were eliminated by the use of two
polished aluminium sheet reflectors mounted as shown in Fig 9 which
prevented light from the sources reflecting directly into the camera.
As a consequence of these reflectors the light intensity was reduced from
1.16×10^1 Wm^{-2} to the required level. The illumination level used
during all the experimental work was 0.233×10^1 Wm^{-2}, measured at the
flume bottom with the tank empty.

Disruption of the sub-surface image by surface wave action was
eliminated by fitting a baffle across the tank. This was attached to
the feed dispenser frame and protruded 2 cm below the water surface
(Fig 3).

Fig 9 Camera and illumination systems.

Top - Position of camera above the flume tank,

plan view.

Bottom - Camera field of view and light paths

associated with the illumination system.

1. Cross-beam, attached to longitudinal beams, Fig 7 (1).

2. Camera and motor drive.

3. Clamp.

4. Vertical support pole.

5. Indicator light (5 watts) attached to cross beam and shielded from
   below.

6. Position of feed dispenser tubes.

7. Baffle "D".

8. Baffle "E".

9. Side walls of flume tank.

10. Housing for illumination system - polished aluminium.

11. Flume tank bottom.

12. Water surface (depth set to 22.0 cm).

13. Warm daylight fluorescent light tubes, 40 w each.

14. Maximum extent of incident light, ray indicates method of
    avoiding reflection into camera lens.

15. Maximum extent of illumination provided by one bank of four
    light tubes. Internal reflections (not shown here) within
    housing (10) resulted in even distribution of light over
    flume tank area.

16. Camera field of view (46°).

PLAN VIEW

THE OPTICAL ENVIRONMENT.

The optical environment that the fish is exposed to is important in that the maximum distance of perception 6f an object depends on the attenuation of the light reflected from it. Attenuation is a function of the molecular structure of the transmitting medium, absorption and scattering within the medium, and the wavelength of the propagated light. Only the latter three are variables in this case. Scattering is predominantly a function of the suspended material, and absorption a function of dissolved material. The variation in attenuation with wavelength causes changes in contrast with viewing distance. Considering a red object and green background for example, the reflected light from these will have peak wavelengths of 675 and 550 nm respectively. In distilled water the Volume Attenuation Coefficients ($\propto$) will be 0.05 and 0.40 m^{-1} (Mertens 1970), which means that there will be a loss in light of approximately 5% and 33% respectively, per metre of optical path. Therefore the contrast between the object and background will decrease sharply with viewing distance due to the different rates of attentuation. A blue object on the green background will not only have a different inherent contrast than the red on green but as blue light attenuates at a different rate to red the contrast will change with distance at a different rate.

The source water used in the flume tank originated as peat mcor run off and consequently contained complex plant material decomposition products in solution, giving a strong yellow appearance to the water. Some suspended material was also present in the water, although the majority was removed by the filtration system.

In order to avoid contrast variation with viewing distance due to differential attenuation it was decided to use prey (object) and background such that the peak wavelengths of reflected light would lie in the part of the visible spectrum where attentuation due to the optical properties of the water was lowest. The food used was a

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deep red colour, pigmented by the dye Amaranth (Trisodium 3-hydroxy-4-napthalene-2, 7-disulphonate), the absorbance minimum (hence reflectance maximum) of which occurs at 650 nm and above. Fig 10 shows transmittance/absorbance curves for the water and the dye, both were obtained using a spectrophotometer, with distilled water as the reference blank. The backgrounds against which food particles could be seen by the fish were the deep shadow beyond the observation window; the wire-mesh baffle screen, also in deep shadow; and the poorly illuminated pale red flume tank side. In the first two cases therefore differential attenuation was avoided as the background did not reflect any appreciable light, while the neutral side wall colour reduced this effect considerably.

The major variable affecting light transmittance was found to be the concentration of fine suspended material that could not be removed by the filtration system. The visibility of different sized food particles to the observer was used as a test to standardise conditions of water clarity. A 0.10 cm diameter food particle when released into the water flow from the most distant feed dispenser (resulting in an optical path of 1.00 m through the water) was found to be the minimum size visible at maximum water clarity. This performance could not be improved upon and experiments were only conducted when these conditions prevailed, and were abandoned if clarity dropped below this standard.

To define the optical environment in a comparative sense, measurements of attenuation were taken at the end of the experimental series. Two types of measurements were made: to determine the total optical attenuation and the variation in attenuation with wavelength respectively. The appropriate factors were calculated from the Beer-Lambert Law:

$$T = e^{-\alpha d}$$

where T is the transmittance over an optical path of length d metres,

and α is the attenuation factor/coefficient. Hence:

$$\alpha = \frac{-1}{d} \ln T$$

I) Percentage light transmittance over a standard optical path length (of 1.00 m) was measured using a Model 912S Transmiss-ometer (Hydro Products, San Diego, California). This instrument used a standard white light source hence light transmittance was measured over the entire visible light spectrum. The Optical Attenuation Factor (α^{-1}) found with the recirculating pump on, ball valve three-quarters open, and under the standard conditions of water clarity was 1.514 ± 0.033 m^{-1} and transmittance was 0.22. Under static water conditions the transmittance increased to 0.30 ($\alpha^{-1} = 1.204 \pm 0.026$ m^{-1}) indicating a substantial contribution to attenuation by material kept in suspension by the water current.

II) Percentage transmittance in static water as a function of wavelength was measured using a spectophotometer of path length 0.01 m. The variation in the Volume Attenuation Coefficient (α) with wavelength is shown in Fig. 11. The use of distilled water as a reference blank introduced the errors indicated, the total values of α for each wavelength being the sum of the two values (not indicated). The distilled water data was adapted from Mertens 1970. The high level of attenuation in the blue-green part of the spectrum (425-575 nm) is the effect expected due to the dissolved material and explains the unusually high values of α^{-1} obtained. For comparison oceanic water containing a low concentration of pigmented solutes but a high level of suspended material characteristically has α values of 1.0, 0.4 and 0.8 m^{-1} at 400, 550 and 700 nm respectively (Mertens 1970).

To sum up, prey colour was chosen such that light propagation interference due to the optical properties of the water was minimal, thereby assuring near constant relative contrast between prey and background with variation in viewing distance. All investigations were conducted at a standard level of water clarity in order to assure reproducibility of optical environment between experiments.

Fig 10. Absorbance of flume water sample and solution of
Amaranth (10 mg l^{-1}). Distilled water reference blank.

Fig 11. Volume attenuation coefficient (α) of flume water
sample calculated from percent transmittance data.

(a) — Absorbance (water sample) WS and Absorbance (amaranth) A versus Wavelength (nm)

(b) — γ (m^{-1}) versus wavelength, showing VISIBLE SPECTRUM between Ultraviolet and Infrared, Distilled water.
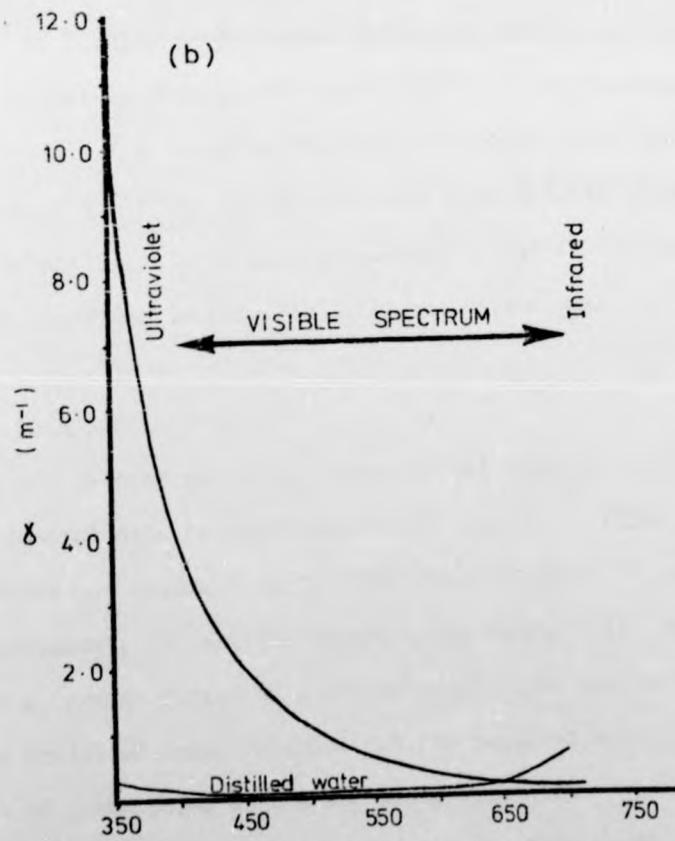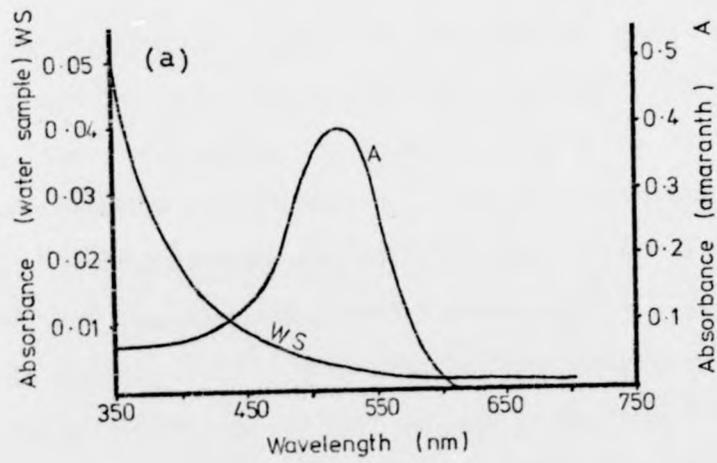
PHOTOGRAPHIC EQUIPMENT

A 35 mm Nikon (Nippon Kogaku K.K., Tokio) F2 Photomic camera
fitted with a 50 mm f/1.4 lens was used. The film wind-on and shutter
release were motor driven and remote-controlled and the camera body was
fitted with a magazine back with a maximum film capacity of 3.3 m
(250 frames). The camera system, excluding the power pack, was
mounted on an adjustable cradle fitted to a vertical sliding arm and
column attached to the vibration-free frame (Fig. 9). A firing speed of
up to 5 frames sec^{-1} was available, and 4.3 frames sec^{-1} was used in all
experiments as this was found to give suitable frame separation.

Kodak Tri-X film (400 ASA/22 DIN) was used in 250 frame lengths.
This was normally rated and exposed at f/2.8 at 1/125 sec. The film was
over developed for 4 minutes at $20^{o}C$ using a high-contrast developer
(Kodak D19). By developing for contrast it was possible to resolve feed
particles of diameters down to 0.1 cm. Each frame represented an
experimental area 1.0 m x 0.67 m (Fig 12). A shielded low wattage bulb
was mounted above the flume within the frame area and its illumination
was used to label the film between sequences. A number was placed on
the bottom of the flume in order to label each frame with the film
number.

PHOTOGRAPHIC DATA PROCESSING.

A complete written record was taken during filming in order to
relate experimental data to each behavioural sequence. Films were
developed, fixed and examined as full 250 frame lengths. Negatives
were used throughout, no positive prints being taken. Film was mounted
in spools on a carrier fitted to a conventional slide projector. Each
sequence was projected frame by frame and the required data traced onto
large sheets of graph paper at a known scale reduction (normally 1:0.64).
Data relating to a particular treatment (e.g. one feed particle size and
one fish) could thus be obtained as a series of feeding sequences on one
sheet. Further tracings enabled the required data to be extracted and

integrated over any number of fish or feeding sequences.

Fig 12 Camera field of view.

1. Baffle "D".

2. Position of feed dispenser array.

3. Baffle "E".

4. Side wall of flume tank.

5. Locating holes in flume tank bottom.

6. Shielded indicator light (mounted above tank, thus not in focus)

7. Film/experiment number.

— Outer margin of film frame.
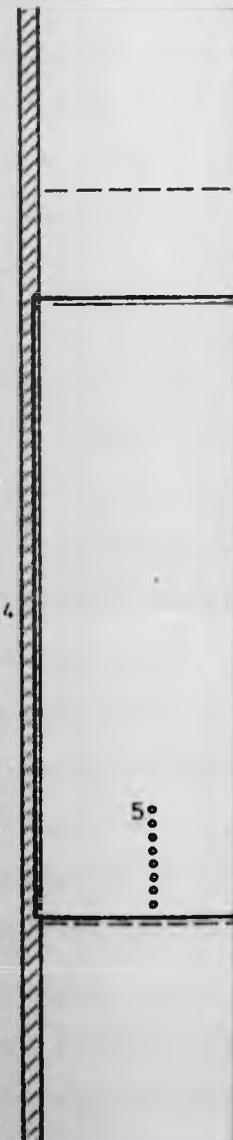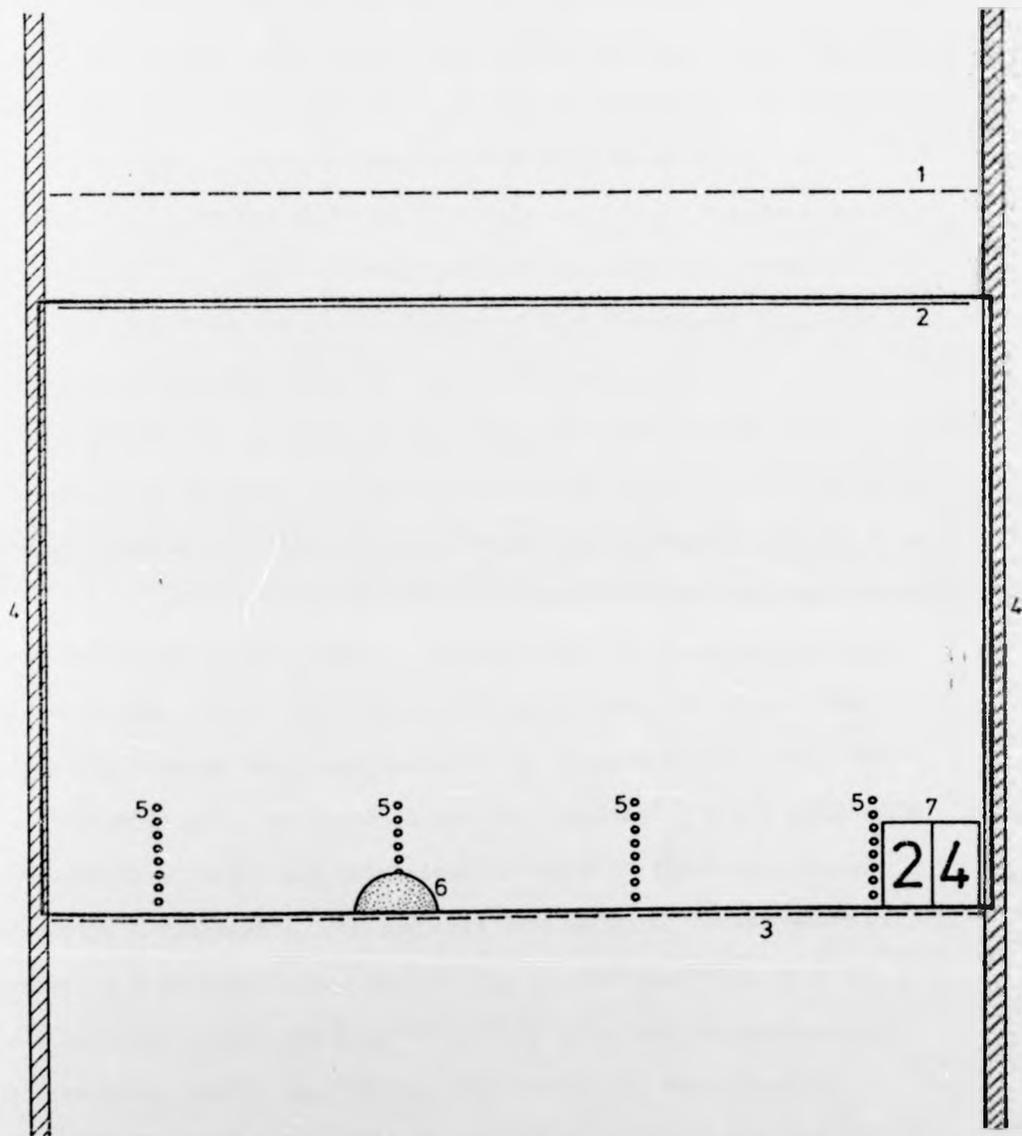
EXPERIMENTAL PROCEDURE AND RESULTS

Three series of experiments were conducted and are listed in Table 1. Those of August and September provided data on the response of the same stock to the same relative feed particle size. The growing season was taken to end at the beginning of September (See Chapters 1 and 4) at which time water temperatures dropped to $7.5^{\circ}C$ and subsequently remained below $11^{\circ}C$, slowly dropping. The June series demonstrated the change of response with feed particle size.

1) Reaction and strike fields of fish feeding on the optimum feed size during and after the end of the growing season.

Fifteen fish of similar size were selected from the stock tank and placed in the holding area of the flume. The size chosen represented the approximate mean length of the stock tank population at the time. Fish in the holding area were fed only during the feeding experiments when non-ingested food, passing through from the experimental area, was available. Fish were held for 8 to 10 days, the actual time depending on when they were used for the feeding experiments. The recirculation pump was switched off for the first 5 days, although a throughflow of water was maintained by means of the ball-cock and standpipe arrangement. The pump was then switched on and water velocity gradually increased during the 6th day to that resulting from the $\frac{3}{4}$ open ball valve position (Fig. 5). Fish were left to acclimate to this velocity during the 7th day and feeding behaviour testing commenced on the 8th day. The $\frac{3}{4}$ open valve position was used as it had been found to provide a current velocity against which fish maintained bottom-associated stations without actively swimming but within which they were also able to swim freely.

One fish at a time was transferred through the hatchway, to the experimental area and allowed 4 hours to acclimate to the new environment, during which it was tested for feeding response. If this proved positive then the experiment commenced, if not then the fish was removed and another

TABLE I Summary of experiments conducted

Date 1976	Mean Fish Length & Range cm	Number of Fish	Food Particle Size Range cm-diam	Total No of Trials Filmed	Flume Water Temp. °C	Loch Water Temp. °C	Flume Water Depth cm	Description of Experiment
11-14 Aug.	5.36(5.1-5.6)	5	0.170-0.200	50	19.0 ± 0.5	17 steady	22.0	Reaction field and Forage area shape and seasonal change.
21-28 Sept	8.08(7.8-8.3)	4	0.236-0.280	35	16.0 ± 0.5	10 dropping	22.0	
08-23 June	8.62(8.1-9.4)	10	0.100-0.118 0.140-0.170 0.200-0.236 0.400-0.470 0.800-0.950	11 33 30 24 25	19.0 ± 1.0	14 rising	22.0	Particle size effect * Also analysis of reaction and capture patterns (Ch.3).

transferred. A 12 hour day - 12 hour night lighting regime (falling within the normal day) was used throughout, and all testing was accomplished between the 5th and 11th hour of "daylight". One food particle was placed in each of the 23 feed dispensers prior to transfer of the fish to the experimental area. Fish were not disturbed during acclimation nor during the experimental period, all necessary manipulations being accomplished from the observation room.

Each trial consisted of the release of one food particle and the filming of subsequent events. Filming commenced as the particle left the guide tube, and continued until it was captured and subsequently ingested or rejected, or until it reached the baffle at the rear of the experimental area. A period of 5 to 10 minutes was allowed between trials. Feed dispensers were actuated in a random order. The end of the film represented the termination of the trial series on that particular fish, which was removed and its fork-length measured. Feed dispensers were then refilled, the camera re-loaded, and the next fish transferred to the experimental area. Not all the fish held in the holding area were used.

Film sequences were processed as described. When transferring data the station held by the fish, prior to any feeding response, was plotted in the same position in all cases. Each capture point could thus be plotted in relation to a single fish commencement point or station. The result was the presentation of prey capture points as a scatter surrounding the station. The outermost points of this scatter designated the maximum extent of the strike field, i.e. maximum striking distance in particular directions. Capture points were plotted irrespective of subsequent ingestion or rejection of the food particle by the fish.

A similar scatter was plotted for the prey position at first response from the fish, irrespective of subsequent events. This was designated the reaction field. This first response was always the

turning of the head towards the prey. Subsequent to this the fish either returned to an upstream facing posture or immediately moved off towards the food. After the commencement of a potential capture sequence fish were found to sometimes abandon this and return to their original station.

Figs 13 and 14 show the reaction and strike fields found. Each point represents one fish and prey interaction. All points originally to the left of the fish have been transposed to the right. It should be noted that the conventionalised representation of the fields shown on the left of each diagram are there solely to place emphasis on aspects of the results thought to be of importance. Table II lists comparative data and gives a breakdown of response behaviour. Maximum reaction field angles are measured from field edge to field edge, and were established between lines drawn through the furthest outlying points of the field and the eye centres of fish at the station.

The premise that points of first reaction and capture might be influenced by the order of feed particle release, expressed through the hunger-satiation state of the fish, was examined by inspection of capture sequences and feed release order. No pattern with feed release order could be established. It is unlikely that after 7 to 10 days starvation fish would show satiation effects after at most 9 food particle captures. Experiments involving feeding to satiation showed that at a temperature of $15^{\circ}C$ fish of approximately 8 cm length starved for one week would consume in excess of 20 food particles of $0.237 - 0.280$ cm diameter before a predominantly rejective mode of behaviour occured.

TABLE II. Reaction field, (R.F.) strike fields, and response summary, 11 to 14th Aug and 21 to 28th Sept.

Experimental series	Maximum R.F. angle	Linear extent of R.F., cm.			Strike Field cm²	Capture + ingest	Capture + reject	No capture	No response
		In front	Maximum to side @ angle *	To side @ maximum R.F. angle **					
11-14 Aug	128	56.5	64.5 @ 76	57.5	4880	9	23	6	12
21-28 Sept	136	36.0	45.0 @ 90	19.5	130	3	6	5	21

NB. * Angle measured from fish mid-plane (ie. parallel to water flow direction).

   ** Angle measured from fish mid-plane to outer margin of Reaction Field.

2) The effect of feed particle size on the Reaction and Strike Fields.

The experimental procedure has been described in the previous section. Ten fish were used in two batches of five in order that extreme starvation of some could be avoided. Five different prey sizes were used. The method of data analysis already described was applied, the results of each feed particle size being treated separately.

The mean internal mouth breadth of the fish used was found to be 0.60cm (range 0.57 to 0.65). This was measured on freshly killed specimens at the widest point in the lateral plane of the mouth (see Chapter 3 for further details). Feed particle sizes were chosen such that they represented a range from appreciably larger than mean mouth breadth to below that on which fish showed maximal growth (Chapter 4). The prey size range originally chosen included 0.100 - 0.118 cm diameter prey as the smallest size but fish rarely responded to this, even when particles passed within snapping distance. Experiments with this feed size were therefore discontinued and the 0.140 - 0.170 cm diameter size substituted.

Due to the higher sinking rate of the larger feed particles used in this experiment it was found necessary to maintain water velocities at the level resulting from the ball valve being $\frac{1}{2}$ open (Fig 6), rather than three quarters as in the previously reported experiment.

Each fish was tested with two feed sizes, which were assigned to alternate feed dispensers. Dispensers were actuated in a random sequence but such that at the end of a series of trials with one fish the two feed sizes were equally represented. One of the two was carried over to the following series of trials (on the next fish) in a way such that a new feed particle size was carried over each time. Each series of trials was arranged so that the particle size that each fish

TABLE III. Title and columns as above, for experimental series 8 to 22nd June.

Food particle size range cm diam	Maximum R.F. angle	Linear extent of R.F., cm.			Strike Field cm²	Capture + ingest	Capture + reject	No capture	No response
		In front	Maximum to side @ angle	To side @ maximum R.F. angle					
0.100-0.118	-	-	-	-	-	2	0	0	9
0.140-0.170	156	51.0	60.5 @ 110	54.5	2800	24	0	0	9
0.200-0.236	154	56.5	83.0 @ 112	78.0	5540	23	1	1	5
0.400-0.475	118	44.0	83.0 @ 118	83.0	2620	2	17	0	5
0.800-0.950	102	12.0	83.0 @ 102	83.0	NONE	0	0	21	4

first captured was the size carried over from the previous trial series. This was done to ensure that if the motivational state of the fish was affected by the first feed particle it was exposed to then any pre-determination of subsequent behaviour would be equally represented between all the feed sizes.

Figs 15, 16, 17, 18 and 19 show Reaction and Strike Fields of fish feeding on the five feed particle sizes. Table III lists comparative data and response behaviour. The following are brief notes outlining major differences and similarities between the feed sizes.

0.100 - 0.118 cm diameter. (Fig. 15).

Fish showed a very restricted and erratic response to this food particle size and little photographic information was obtained. From additional observations made it would appear that both the reaction field and strike field were restricted to within about 1.5 fish body lengths of the station held.

0.140 - 0.180 cms diameter. (Fig. 16).

Initial response was always followed by capture and ingestion, thus the strike field extended fully over the area downstream of the reaction field. The maximum reaction distance was the shortest found in this series, although the field angle was the greatest and equal to that shown by fish feeding on the 0.200 - 0.236 cm size.

0.200 - 0.236 cms diameter. (Fig. 17).

Initial response was almost always followed by capture and ingestion. The maximum reaction distance was equal to, but the reaction field was larger than that of fish feeding on the larger prey sizes. The reaction distance was greater than and field angle equal to those of the 0.140 - 0.180 cm feed size results. The strike field was correspondingly far larger, approximately twice the area of any others.

0.400 - 0.475 cms diameter. (Fig. 18).

The reaction distance was found to be equal to, but the field

angle smaller than that obtained with the 0.200 - 0.236 cm feed size. Similarly the strike field area was smaller although it extended laterally for the same distances as the reaction field. Except for two items all feed particles were rejected after capture. Again in all cases of initial response subsequent capture took place. Initial response in all cases bar one took place within 25 cm of the feed dispenser array, in contrast to the previous two feed sizes.

0.800 - 0.950 cms diameter. (Fig. 19).

Fish responded to 84% of the feed particles presented although none were captured. In 16 cases a positive response was abandoned by the fish after a head-turn or within one body length (bl) of its station. In the remaining 5 cases the fish turned away before reaching the food. Thus there was no strike field. The reaction field was very fragmented, feed particles directly in front of the fish eliciting no response until they were within 1.5 bl of the fish, while most of the initial response reactions took place within 25 cm of the feed dispenser array (Cf. 0.400 - 0.475 cm feed size). Maximum angle was much reduced in comparison with the other feed sizes.

Figs 13 - 19 Reaction and Strike Fields

Legend Prey position at first response   ○

Point of prey capture   ●

Trajectory position of prey not   ▼
responded to by fish.

See text for further details

13   0.170 - 0.200 cm prey diameter, 11 14 Aug

14   0.236 - 0.280 cm prey diameter, 21 - 28 Sept

15   0.100 - 0.118 cm prey diameter

16   0.140 - 0.170 cm prey diameter

17   0.200 - 0.236 cm prey diameter

18   0.400 - 0.475 cm prey diameter

19   0.800 - 0.950 cm prey diameter

13

10cm

14

10cm

15

10cm

16

10cm

10cm

17

18

10cm

19
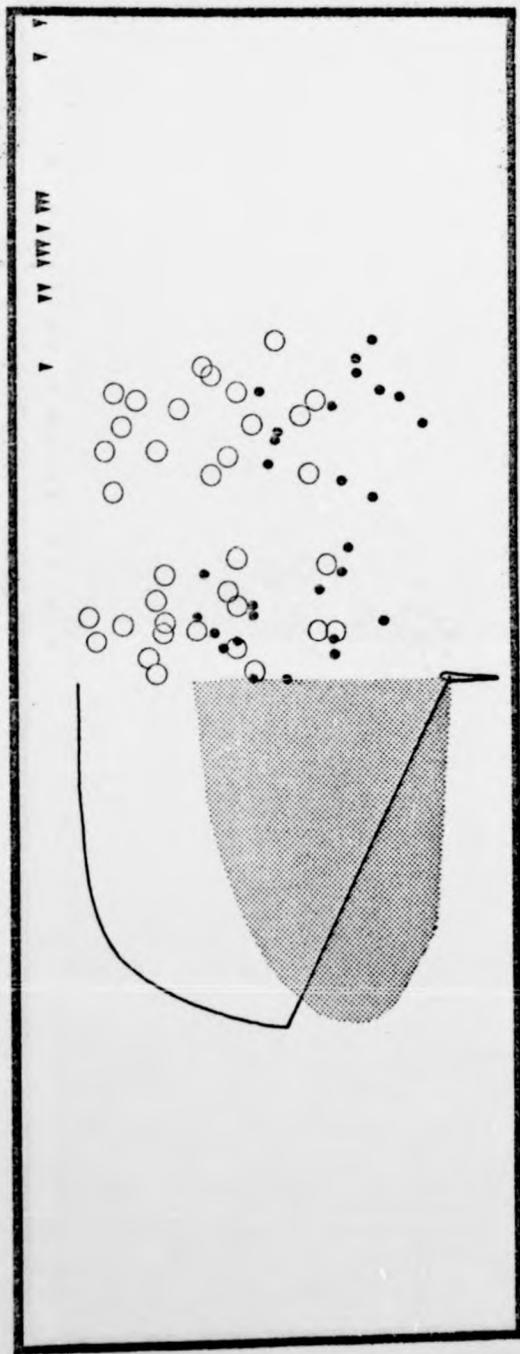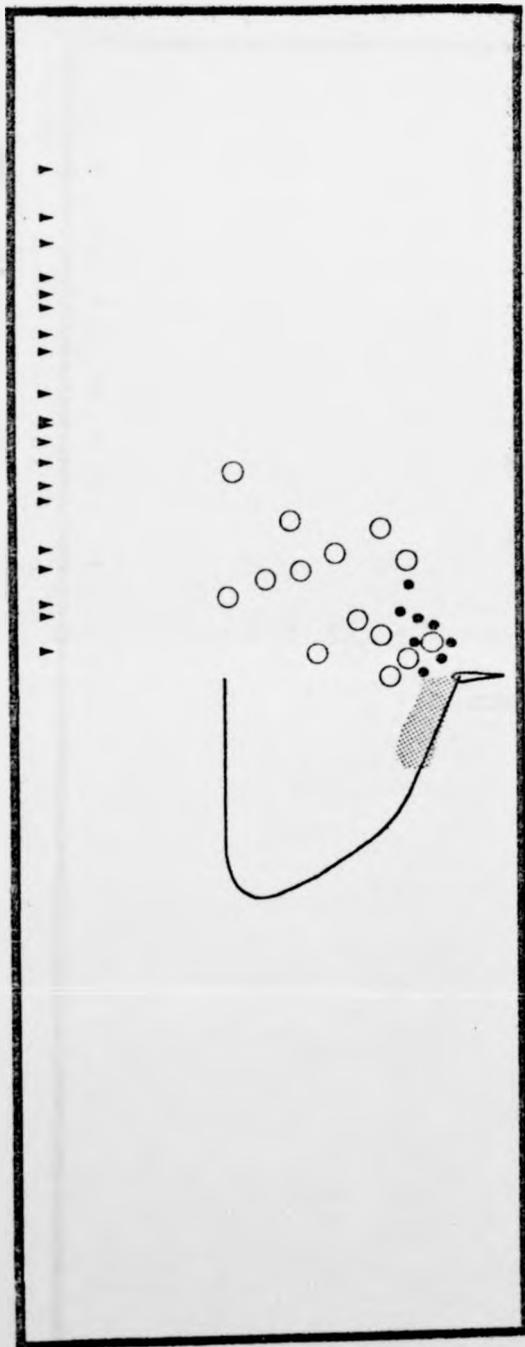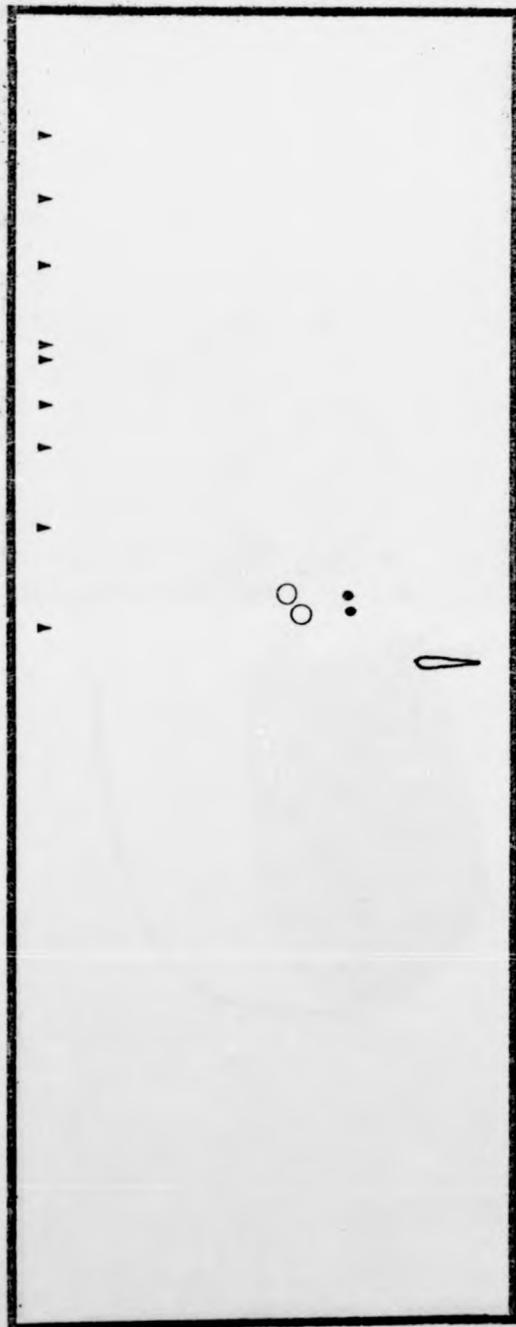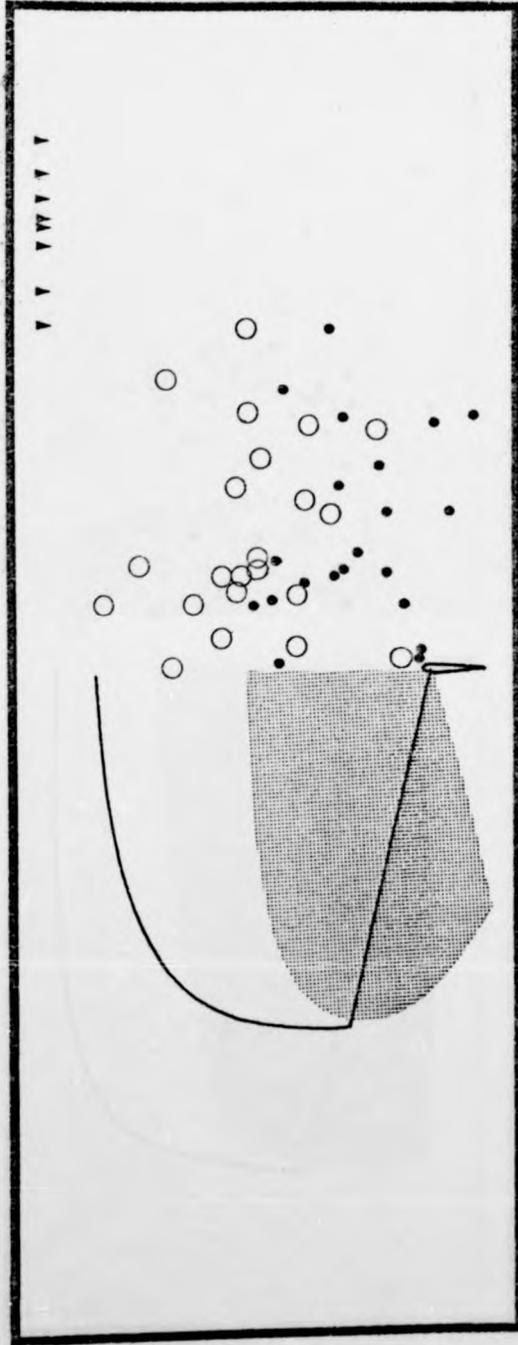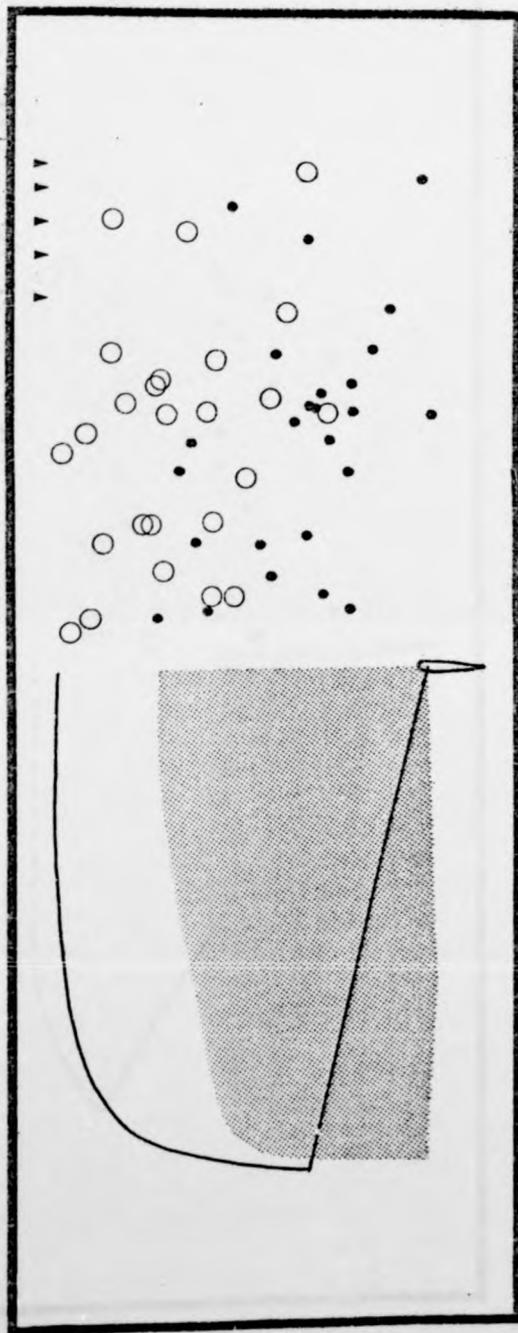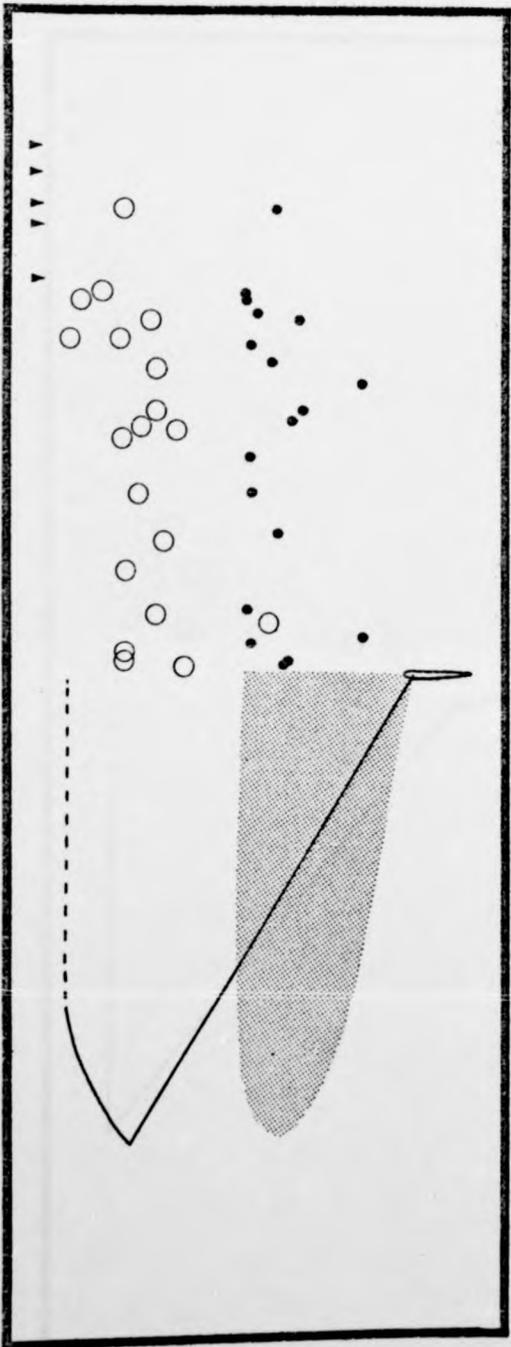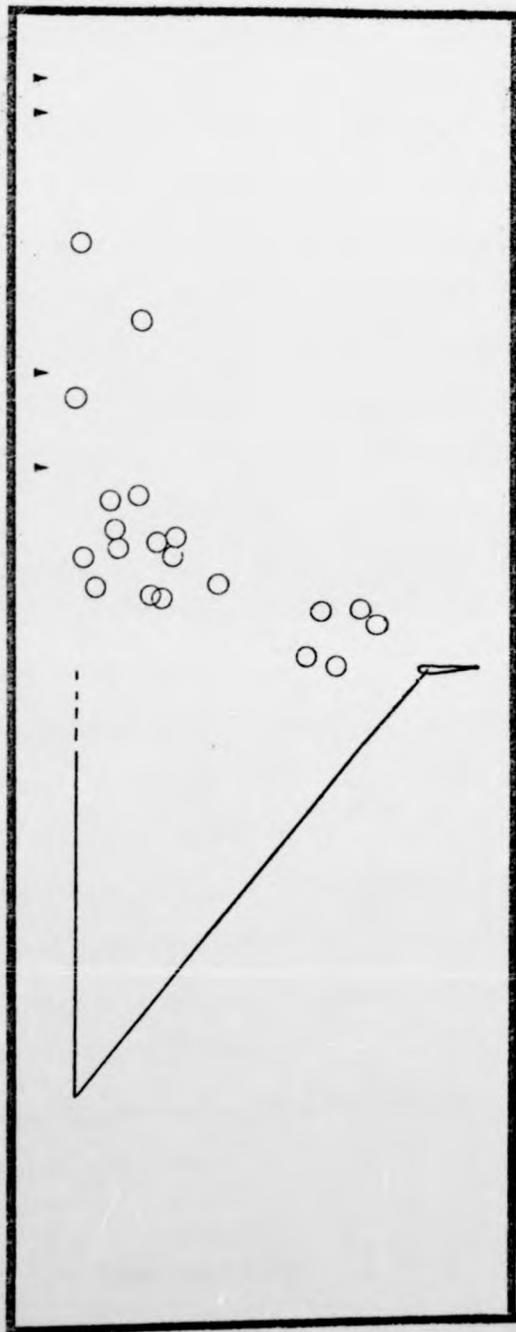
10cm

THE SALMONID VISUAL SYSTEM

Eye Orientation During Feeding.

An analysis of horizontal head orientation with respect to prey position.

Polyak (1957), Pumphrey (1961), Hester (1968) and Protasov (1968) review evidence for, and theoretical aspects of, binocular (i.e. stereoscopic) visual fields in fish. Observations of eyeball rotation in the anterior-posterior plane showed it to be restricted to a few degrees of movement, in the freely active (i.e. not anaesthetised) fish. Thus the longitudinal axis of the head, viewed from the dorsal side of the fish, is closely related to (though does not necessarily correspond with) the visual axis orientation. A restricted range of head axis-food particle position angles, provided this was not due to body axis alignment resulting from swimming activity, would strongly indicate a preferred zone of vision.

An analysis of the results of the trials with the 0.200-0.236 cm diameter feed size was made to determine the head axis direction with respect to food particle position. Table IV lists the results of these measurements, taken frame by frame. As can be seen 77% of observations fall within $\pm$ 4 degrees, 100% within $\pm$ 10 degrees. In most cases the body and head axes were not coincident and the head was turned in the direction of the food item.

An analysis of eye movements in rainbow trout juveniles feeding in static water conditions.

METHODS

Several rainbow trout (Salmo gairdnerii) juveniles averaging 10 cm in length were trained to accept food pellets in the presence of laboratory staff. These fish were maintained in separate aquaria (30 x 30 x 40 cm in size) into which fresh water was passed, by means of a pipe reaching to the bottom of each, at a rate of approximately 0.5 l min^{-1}. These fish belonged to, were kept and trained at the

TABLE IV. Horizontal angle between head longitudinal axis* and food particle position**.
Observations include only those taken during fish swimming towards food, i.e. from
one film frame after initial head-turn to immediately before food capture.

Experimental series 8 - 22 June, 2.00-2.36 mm feed size range only, film speed 4.3 f.p.s.

Degrees (inclusive)	>+10	+10/+8	+7/+5	+4/+2	+1/-1	-2/-4	-5/-7	-8/-10	<-10
Number of frames	0	6	7	19	46	20	11	2	0

NB + upstream of food-head axis

    − downstream of food-head axis

* Tip of snout to mid-point between opercula

** Axis of food particle centre and mid-point between eyes

University of Stirling Department of Biology.

During the experiment fish were fed on pre-immersed food pellets (Cooper Nutrition Products, Witham, Essex) and behaviour subsequent to food introduction was filmed through the side of the tanks using the Nikon motor driven camera system already described. Kodak Tri-X film was used, at camera settings of f4.0 and 1/500 th sec, and a film speed of 4.3 f.p.s.. Illumination was provided by two 55 Watt quartz-halogen lights suspended 1.0 m above each tank. No measurement of light intensity within the tanks was taken. Three fish were used and a total of 20 feedings were filmed; 10 of these films proved suitable for analysis, which was performed in a similar manner to that already described (i.e. by projection and tracing).

Several attempts had been made at training salmon juveniles to feed in the presence of an observer. All had failed. Light attenuation through the "one-way" glass system of the flume tank apparatus was of such a high order that additional illumination was required for successful photography and under this the fish did not feed. In addition the fish to camera distance was such that close-up photography was not possible through the glass with the Nikon camera system. Considerable footage of fish feeding in the flume tank was in fact taken by Edinburgh Studios Ltd. (Penicuick, Edinburgh) using professional low light intensity 16 mm colour cine equipment. The result, although suitable for gross analysis of behaviour (Chapter 3), lacked the detail necessary for an analysis of eye movements.

RESULTS

Figs 20 and 21 show outline tracings of four representative capture sequences illustrating food capture above and below the original position of the fish. Of interest here is the orientation of the longitudinal axis of the eye, taken as the line of maximum pupil diameter in the anterior-posterior plane of the eye.

As can be seen from these Figs and Table V there was no

Fig 20 & Fig 21   Two examples of film sequences of rainbow trout
capturing food particle showing axis of eye in
relation to particle position. ($1\frac{1}{2}$ x natural size,
filmed at 4.3 f.p.s.).

Top   Capture above original fish position
Bottom   Capture below original fish position

trout
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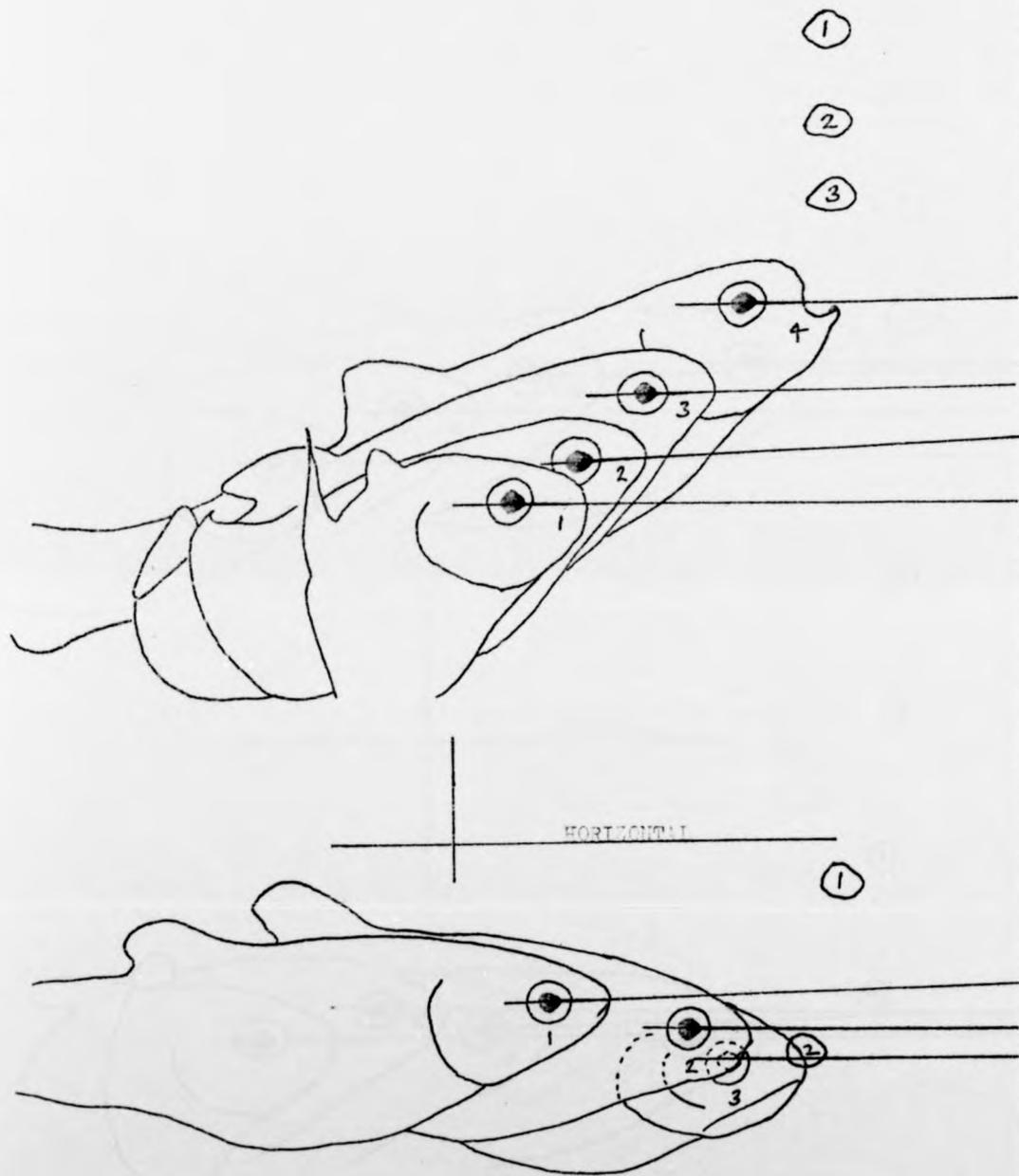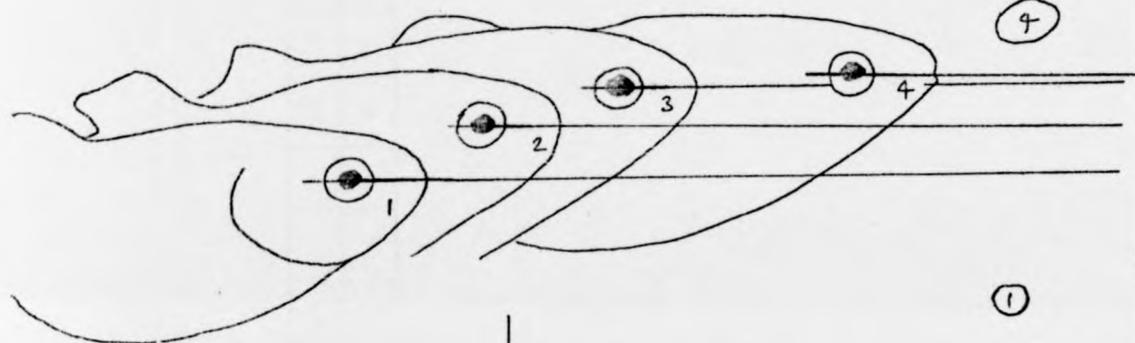
HORIZONTAL
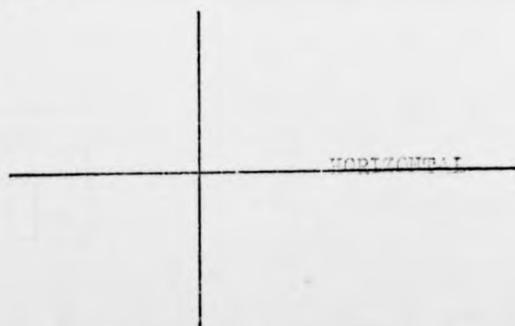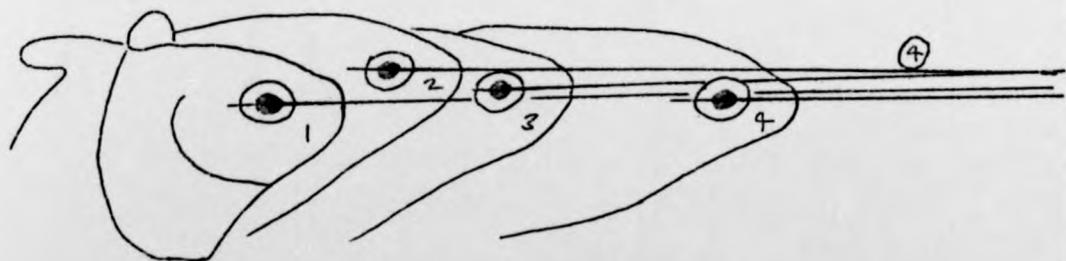
HORIZONTAL

TABLE V. Vertical angle between longitudinal axis of pupil and horizontal plane. All film frames up to food capture. Three trout, 10 feeding sequences, film speed 4.3 f.p.s.

Degrees	+4	+3	+2	+1	0	-1	-2	-3	-4
Number of frames	0	2	4	4	14	4	1	0	0

correspondence between food position(relative to the fish)and eye axis direction. The longitudinal axis of the eye in all cases remained within ± 3 degrees of the horizontal plane, 76% of observations falling with ± 1 degree. Furthermore the angular displacement of the head from the horizontal had no effect, the eye rotating in the dorso-ventral plane such that the longitudinal axis remained horizontally placed.

Description of the Visual System.

Eye Structure (Fig 22)

i) Cornea and anterior chamber.

The cornea is a transparent membrane enclosing the anterior chamber of the eye and serving a protective function. It is convex in shape and in salmonids has a definite rostral bulge (i.e. when viewed from above it has the shape of a longitudinal section of a chicken egg, the blunt end pointing rostrally). The refractive index of the cornea/anterior chamber is very similar to that of water (1.377 as compared to 1.33), therefore is clearly optically inert and unlikely to play any part in vision (Tamura 1957).

ii) Iris membrane.

The iris membrane is inclined about 5 degrees allowing rays at 95 degrees to the principal optical axis to enter the eye (Polyak 1957, Trevarthen 1968). It is not capable of photomechanical changes and thus the pupil is of fixed size (Ali, 1959). The pupil shape is shown in Fig 23. The antero-posterior diameter of the pupil was found by measurement to be a mean of 0.14 mm greater than the dorso-ventral in all sizes of fish (Fig 23).

iii) Posterior chamber.

The vitreous humour contained in the posterior chamber is continuous with the aqueous humour in the anterior chamber, has a similar refractive index and is therefore also optically inert (Tamura 1957).

iv) Lens.

The crystalline lens is accurately spherical and unchanging in shape. It has a short focal length of approximately 2.5 times its radius and a correspondingly large aperture of f/0.8. It is clear and free from internal discontinuities, scattering or surface reflections. It is also free from spherical aberration and almost free from chromatic aberration. The lens is the only optically active component of the

Fig 22. Horizontal section of salmonid eye (adapted from
Protasov 1968 and Polyak 1957).

Legend: r.b. rostral bulge of cornea

corn.   cornea

ret.   retina

ln.   lens

a.ch.   anterior chamber

Ir   iris diaphragm

p.ch.   posterior chamber

P.A.   Principal axis

S.A.   Secondary axis

Fig 23. Lateral view of salmonid eye.

Legend: as above

b = 0.9950a+0.1387;   r=0.9925;   P < 0.001

salmonid eye.

v) The retina.

In the Pacific salmon retina, which is considered to be essentially similar to that of the Atlantic salmon (Ali 1959, Ali et al 1961), nine distinct layers can be isolated (Ali 1959, Nicol 1975). The visual cells are of both types, namely rods and cones, and both single and twin cones are present (Ali 1959). The visual cells are protected from excessive light by radial migration of their terminal segments and counter-migration of the pigment in the pigment epithelial cell layer (Pumphrey 1961, Ali 1959, Nicol 1975). No fovea as such has been identified (Ali 1959) although areae of high cone density have been found in many fish (Yamanouchi 1956, Tamura 1957, Pumphrey 1961, O'Connell 1963) including trout (Polyak 1957). It would appear that at least in the trout the retina is elliptoid in shape, the antero- posterior axis being some 3% longer than the dorso-ventral (Pumphrey 1961).

The main function of the visual system is twofold:

I) A perception of space within which the fish can orientate itself

II) The identification and localisation of objects of potential interest within that space.

Two main factors are involved, namely accommodation and acuity, which together determine the shape and nature of the visual field:-

Accommodation.

Depending on species and methodology of experiment, teleost fish eyes are either myopic, emmetropic or hyperopic when in a resting state (Schwassman 1975). In fish accommodation is accomplished by movement of the lens by contraction of the retractor lentis muscle complex. In a few species the direction of movement is along the pupil axis (e.g. Carassius auratus), in the majority the main movement occurs close to the plane of the pupil (e.g. Salmo trutta) although not directly along this plane since some lens motion is still found in the direction of the pupil axis (Pumphrey 1961, Sivak 1975). In this way near or distant

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objects are brought into focus on definite parts of the retina.
Movement of the lens rostrally (i.e. in the pupil plane) brings objects
into focus on the temporal retina. Tamura (1957) found that the direction
of displacement coincided with the   visual axis   and
this aspect will be further considered in the section on visual fields.
It would appear that most species of fish can focus for sharp vision up
to infinity, and the near point of accommodation varies from 0.1 to 50.0 mm
depending on the size of the fish (Bogatyrev 1966). Pumphrey (1961),
considering theoretical implications of accommodation, has calculated
that for a lens of focal length 5.0 mm the amplitude of movement would
not need to exceed 0.3 mm to give the performance required.

Visual acuity.

Acuity is normally measured in terms of the lowest limits of
resolution, i.e. sufficient to produce a detectable difference in
retinal stimulation by comparison with the surrounding field, and
consequently defined as the angle, measured at the eye, subtended by the
smallest detail (Pirenne 1962). In an absolute sense it depends on
two factors, namely the optical image on the retina and the pattern of
excitation produced in the retina and optic tectum. Variation in
acuity will occur with light intensity, stimulus-background contrast,
and the state of retinal adaptation amongst other factors (Riggs 1966).
It is worthwhile discussing these three factors first before considering
structural limits to resolution.

In Atlantic salmon complete retinal adaptation (hence full visual
acuity, Ali 1959) takes about 45 mins (Ali et al 1961) and full light
adaptation is reached at 10^1 lux (Ali 1961). In fish, rods have such
a low light threshold (e.g. Brunner 1934) that cones are of overwhelming
importance in form perception. Brunner (1934) found that visual acuity
of Phoxinus laevis increased in proportion to the log of the light
intensity and maximum acuity was reached at a fairly low light intensity
(approximately 12 to 35 lux). Hester (1968) found that the contrast

(between object and background) threshold required to elicit a response from conditioned goldfish decreased with increasing diameter of object. He also found that the contrast threshold varied with the adaptive state of the eye.

The resolving power of the dioptric mechanism depends entirely on the crystalline lens as this is the only optically active component. Yamanouchi (1956) found the minimum optical angle of resolution in the coralfish (Microcanthus japonica) to be 4'59". The minimum optical angle of resolution seems to be a function of lens diameter, Tamura (1957) reported that lenses larger than 5 mm diameter had a resolving power of 54" to 1'30", those of less than 5mm less than 2'0" to 2'10" (means of measurements on 27 species of marine teleosts).

The resolving power of the retina appears to be the main influence on acuity, and depends on the distance between adjacent cones bearing separate neural connections. However, the cone spacing is not uniform over the retina, there being well-defined areae of high cone density in most fish species (Yamanouchi 1956, Tamura 1957, O'Connell 1963 and Hester 1968). Yamanouchi (1956) found the highest cone density in Microcanthus in the temporal region, the cone spacing corresponding to a minimum angle of resolution of 3'36". Tamura (1957) found areae in the dorso-temporal, temporal and ventro-temporal regions of the retina, the location depending on the species, and the resolving power varying between 4.2 and 15.4 minutes. Areae of high cone density, thus enhanced acuity, in the temporal region of the retina would result in maximum visual acuity in the forward part of the visual field, which is also the direction in which accommodation for sharp vision takes place in most fish (Carassius auratus being a notable exception).

Overall visual acuity has been measured in a variety of fish species, the minimum angle of resolution (usually of stripes measured through a conditioned response) varying from 4.2 to 53.0 minutes of arc (Yamanouchi 1956, Tamura 1957, O'Connell 1963, Weiler 1966, and Protasov

1968) depending mainly on species but also on the size of the fish within one species. Variations in acuity between fish species correlate closely with variations in cone spacing and not lens size. Within one species visual acuity increases with length of fish, lens diameter also increases while cone density either declines (O'Connell 1963) or remains almost constant (Baerends et al 1960, Hester 1968). The minimum angle of resolution has been found to change in proportion to lens diameter (Yamanouchi 1956, and Baerends et al 1960) as has the contrast threshold, a measure of acuity (Hester 1968).

Measurements of the eyes of 56 Atlantic salmon 2.6 to 27.0 cm in length (x) have demonstrated that eye (y_1) and pupil diameter (in the antero-posterior plane, y_2) show different rates of negative allometric growth with respect to fish length ($y_1 = 0.0300x + 1.70$, $r = 0.9700$; $y_2 = 0.0200x + 0.7230$, $r = 0.9662$, both at $P < 0.001$), such that the pupil diameter/eye diameter ratio decreases with increase in fish length. As can be seen from Fig 23 pupil diameter is a reasonable approximation of lens diameter for these purposes, and thus it can be inferred that lens growth is negatively allometric with the growth of the fish. From the above discussion it would follow that acuity is unlikely to increase in direct proportion with fish body length, rather a slight increase would be expected.

Visual fields.

The visual field is a projection of the outside world through nodal points at the centres of the lenses. The shape of the pupil molds the contours of the field such that the extent of the field is increased towards the mid-plane in front and below the fish by means of the pupillary cut-outs (Fig 23). In addition a sighting-groove (Pumphrey 1961) runs from the anterior edge of the eye to the nostril (Fig 24). The eyes are mounted on the upper side of the head and angled towards the anterior of the fish (Fig 24). Measurements on photographs taken from above the fish while swimming towards prey

indicate that the secondary axes (Fig 22) of the eyes converge at a
mean angle to the fish head mid-line of 8.6 degrees (range 5 to 12,
mean of 24 measurements), the point of intersection being a mean of
2.1 cm (range 1.0 to 4.0) from the tip of the snout, irrespective of
fish size (5.0 to 9.2 cm). Thus the binocular field of view subtends
a mean angle of about 17 degrees, and a probable maximum of 24 degrees,
depending on orientation of the eyes in the horizontal plane. This
field would presumably be slightly extended in the zone of the anterior
pupillary cut-out. The binocular part of the visual field is of
importance as it provides the only mechanism for perception of the
spatial relationship between the fish, external environment and objects
therein. In addition there is evidence that the binocular field is a
zone of enhanced perception, the binocular contrast threshold in
goldfish being 0.67 of that of the monocular (Hester 1968). It would
be likely then that the binocular field would represent a preferred
zone, objects of interest being maintained within the angle subtended
by this field. Measurements on the orientation of the head mid-line in
relation to prey being intercepted (p65) show a preferred orientation
of 0 degrees, with a maximum range of $\pm$ 9 degrees (i.e. total angle
subtended was 18 degrees). This is in accordance with that expected
from the foregoing.

Rotation of the eye around the principal axis was found to be
very pronounced (p66). However this was a compensatory movement only,
such that irrespective of head orientation with respect to the true
horizontal the antero-posterior axis of the eye remained horizontal
relative to the external environment. Thus the anterior pupillary
cut-out/sighting groove axis only remains in line with the object under
scrutiny while the head is horizontal and in line with it, tilting of
the head to capture prey displaces the line of sight into a zone of
(theoretically) poorer stereoscopy. This is the reverse of the
behaviour shown by the leatherjacket (Acanthaluteres pilomelanurus)

(Lanskester and Mark 1974) whose longitudinal eye axis remains fixed on the prey by rotation of the eyes relative to the head/body axis which itself is only aligned with the food at the moment of capture.

In the dorso-ventral plane the eyes converge towards the dorsal side of the fish, so that when viewed from above both pupils are visible (Fig 24), while from below the fish the eyes cannot be seen. This orientation would result in greater overlap of the visual fields towards the upper front of the field of view. Thus the anterior pupillary cut-out and sighting groove may be adaptations to increase stereoscopy in a part of the visual field that would otherwise be poorly served. Movement of eyes in this dorso-ventral plane appears to be limited, except for pronounced compensatory movements if the fish is mechanically rotated around its longitudinal axis (Polyak 1957).

The visual axis can be defined as the line of most acute vision, passing from the centre of the area of highest cone density through the centre of the lens (Tamura 1957). Thus fish with areas in the dorso-temporal, temporal or ventro-temporal have visual axes extending, respectively, into the lower frontal, frontal, or upper frontal regions of the visual field. Tamura (1957) found that the line of greatest accommodation appears to coincide with this axis and that the widest binocular angle lay in the plane between the visual axes of the two eyes. In trout there is evidence that areae exist in the temporal region, although the extent dorso-ventrally is not known (Polyak 1957). This, considered with the antero-posterior direction of accommodation, strongly implies a visual axis directed frontally.

Various attempts have been made to derive a two-dimensional representation of the visual field of fish (Pumphrey 1961, Protasov 1968 and Trevarthen 1968) with the eyes in a "resting" state, and with due allowance made for accomodative movements. Fig 25 reproduces two diagrams derived by Protasov (1968) from information on the visual system of trout.

Fig. 24. Head of salmon, showing eye position.

Legend: ns Nostril

s.g. Sighting groove

eye Eye

op Operculum

Fig. 25. Theoretical visual field of trout in the
horizontal plane (Frotasov 1968).

Legend: o Centre of retinal hemisphere

x Centre of lens

P.A. Principal axis

A Back boundary of sharp vision

B Line of focus

C Front boundary of sharp vision

D-D Binocular field

o Centre of retinal
× Centre of lens

op eye s.g. ns

binocular field

A B C D

BACK BOUNDARY OF SHARP FOCUS VISION
LINE OF VISION
FRONT BOUNDARY OF SHARP VISION

PA

D B B D
A A
A A
B B
C C
D D

○ Centre of retinal hemisphere
× Centre of lens

To summarise: the visual fields of each eye subtend an angle of 190 degrees and overlap by at least between 10 and 24 degrees depending on eye orientation. Maximum field overlap occurs along the plane between the visual axes which are most likely directed dorso-frontally, although pupillary cut-outs and sighting grooves increase the binocular field frontally. The visual axes represent the centres of zones of sharpest vision. For each eye only one, albeit quite wide, depth zone is in focus on the retina at any one time. The retina of each eye receives a different image of the external environment and the parallax differences between the two projections on the retinas in the binocular part of the field are potential bases for the perception of depth. Movement of the eyes allows variation in the extent of the binocular field and orientation of the visual axes with respect to the body of the fish, although the eyes always remain horizontally oriented relative to the environment.

Colour vision.

The goldfish visual system has been found to respond to all wavelengths within the visible spectrum (400 to 800 nm., Yager 1968) and similar results have been obtained with Atlantic salmon visual adaptation (364 to 690 nm., Ali 1961). Behavioural experiments have shown that rainbow trout can discriminate between colours (Adron et al 1973, Ginetz and Larkin 1973).

Perception of movement.

Cronly-Dillon (1964, in Arnold 1974) has shown there are approximately twice as many units in the optic tectum sensitive to horizontal as to vertical movement and that specific ganglion cells in the retina respond to the direction of image movement. In goldfish a naso-temporal object movement elicits a stronger cardiac response than one in the opposite direction (Ingle 1968). Thus the visual system appears to be most sensitive to downstream movement of objects with respect to upstream oriented fish. The angular velocity of objects has

been shown to affect response. Boulet (1960) found that as the angular

velocity of a 7 mm sphere was increased from $11°30'$ sec^{-1} to $30°0'$ sec^{-1}

perch would progressively intensify their response in the order, eye,

fin, mouth, body movements, and finally pursuit. All responses were

maximal at $30°0'$ sec^{-1}, and as velocity increased to $65°$ sec^{-1} response

intensity progressively decreased in the reverse order until flight

reactions occured. At velocities above $78°30'$ sec^{-1} and below $11°30'$

all responses ceased.

DISCUSSION

Awareness Distance.

In the flume tank experiment it was found that the minimum angle subtended at the eye by a prey item which elicited a positive response was 8' of arc (Table VI). In the absence of physiological data it will be assumed that this angle represents the minimum visual angle (a) at which awareness of the presence of an object within the visual field occurs. The awareness distance (r_a) at which an object of length L subtends the angle a is given by the equation:-

$$r_a = \frac{L}{\tan a} \qquad \ldots\ldots\ldots\ldots\ldots(I)$$

Fig 26(I) shows the change in calculated awareness distance (r_a) for the range of prey diameters (L) studied. From discussion in the Introduction and Methods sections (pp 38,47) it was determined that object and background colour combinations and differential attenuation within the light spectrum due to the optical properties of the water excerted a significant effect on the awareness distance. As colour combinations were kept constant between all experiments the main effect or r_a with respect to L was optical attenuation.

Two measurement of optical attenuation were obtained and corrections based on these applied to r_a (Fig 26, 2 and 3). The optical attenuation factor is a measurement of total attenuation within the visible spectrum and was found to be 1.514 m^{-1} (p55) which corresponds to attenuation of 78% of the light per metre path length. The mean volume attenuation coefficient between 600 and 700 nm (corresponding to the reflectance peak of the prey) was 0.46 m^{-1} (Fig 10), an attenuation of 36% per metre path length. In both cases the correction was accomplished by extrapolation of curve (1) to a mean prey diameter of 0.100 cm, i.e. r_a = 45 cm taking a to equal 8', and increasing a in proportion to

Fig 26. Awareness Distance (r_x) and prey size.

1. Minimum resolution angle 8', no attenuation.

2. Corrected for 78% attenuation m^{-1}.

3. Corrected for 36% attenuation m^{-1}.

4. Alternative correction for 36% attenuation m^{-1}, increasing target area by 36% m^{-1} (Cf. compens--ation by visual angle increase.p. 78).where target area is the cross-sectional area of the prey item at 90 degrees to the line of sight.
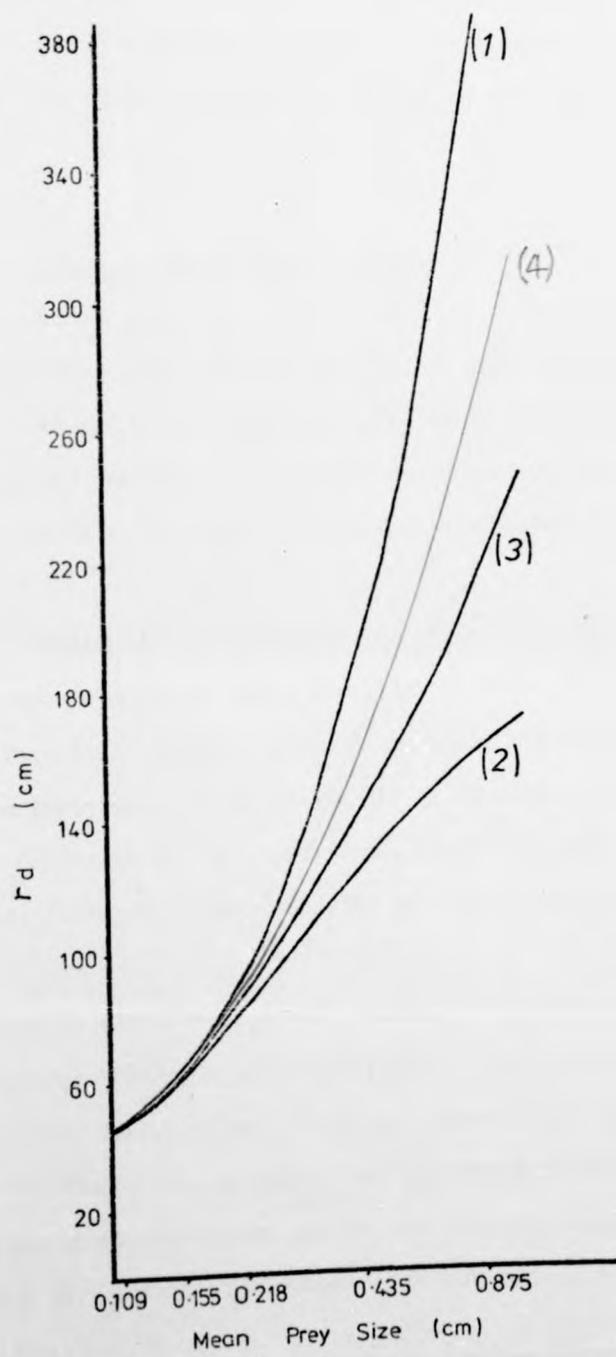
the percent attenuation per unit path length[*], then applying equation
(I) above. From considerations of the prey colour and background
combination (p53) and its effect on attenuation it is likely that
curve 26(3) represents the limits to awareness within the experimental
environment.

Reaction Field.

General considerations and criticism of results.

The shape of the visual field of juvenile Atlantic salmon is not
known. However within this field, for any one size of prey, there will
be (i) an awareness field and (ii) a reaction field which represents
the space within which the prey may be responded to by orientation of
the head and eyes to fix it in the field of sharpest and/or binocular
vision.

The reaction field can be described in terms of three elements,
namely the minimum response angle ($\emptyset$ min), the linear extent of the
field, i.e. maximum reaction distance (r_r), and the angle subtended by
the total field. The importance of these elements in interpreting
reaction field shape and variation with prey size, fish size, and
season will be considered together with comments on the validity of
the results.

The maximum reaction distance (r_r) will depend on the part of
the reaction field through which the prey item passes. Table II and
III list values of r_r (the linear extent of the reaction field) along
three directions in the field. These values are reproduced in Table V
together with the angle subtended at the eye ($\emptyset$, the response angle) by
the prey size to which they refer. The values of $\emptyset$ were obtained from
equation (I), substituting r_r for r_a and $\emptyset$ for $\underline{a}$ $/$ equation (2)$/$

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[*] As 36% of the transmitted light is lost per metre optical path length
it follows that for the contrast threshold (based on $\underline{a}$ = 8' at r_a =45cm
for this prey/background combination) to be maintained this loss of
light must be compensated for. Thus by increasing $\underline{a}$ by 36% m^{-1} the
amount of light incident on the retina from this source remains the
same. The same argument applies to 78% attenuation.

TABLE VI. Summary of prey diameter (L), reaction distance (r_r), and minimum visual angle of response ($\emptyset$).

Date	Fish length cm	Mean L cm	r_r front cm	$\emptyset$ (mean & range)	r_r maximum cm	$\emptyset$ (mean & range)	r_r @ maximum R.F. angle cm	$\emptyset$ (mean & range)	PFR*
11-14 Aug	5.36	0.185	56.5	11'(10 – 12)	64.4	10'(9 – 11)	57.5	11'(10 – 12)	0.0345
21-28 Sept	8.08	0.258	36.0	24'(22 – 26)	45.0	20'(18 – 21)	19.5	45'(42 – 49)	0.0319
08-23 June	8.62	0.109	–	–	–	–	–	–	0.0126
		0.155	51.0	10'(9 – 11)	60.5	9'(8 – 10)	54.5	10'(9 – 11)	0.0179
		0.218	56.5	13'(12 – 14)	83.0	9'(8 – 10)	78.0	10'(9 – 11)	0.0253
		0.435	44.0	28'(25 – 30)	83.0	18'(17 – 19)	83.0	18'(17 – 19)	0.0505
		0.875	12.0	57'(52 – 62)	83.0	36'(33 – 39)	83.0	36'(33 – 39)	0.1015

* PFR Prey/Fish Ratio: $\dfrac{\text{Mean prey diameter}}{\text{Mean fish length}}$

Minimum response angle ($\emptyset$ min).

A plot of $\emptyset$ against L (Fig 27, 8-22 June) shows that all curves flatten off at 9 to 10' of arc. This is thus the minimum prey angle subtended at the eye ($\emptyset$ min) that elicits an overt behavioural response from fish of mean length of 8.62 cm at that time of year. The corresponding value for fish 5.36 cm in length (Fig 27 August) was 10 to 11' from which it can be inferred that fish of this size have a slightly reduced visual acuity compared to fish 8.62 cm in length. This would be expected in accordance with the slight reduction in lens diameter recorded (p 72). Both the June and August experimental series were conducted during the time of the peak growth season (Allen 1969) while ambient water temperatures were rising or steady at a high level (Table I), and as such fish responses are comparable. The results of the experimental series conducted during September show that $\emptyset$ min had increased to approximately twice the June value in fish of comparable size. Whether this represents a reduction in visual acuity, and thus awareness distance, to about 0.5 of its maximum level (as a function of reduced metabolic rate in response to falling water temperatures) or merely a reduction in reaction field extent (see below) cannot be determined on the basis of this data. It is potentially significant, however, that although ambient water temperatures at which fish were held prior to the experiment had dropped to 10°C, and were still falling, the flume water temperature was maintained at 16°C thus eliminating the possibility of a directly temperature-dependant variation.

Reaction distance (r_r).

Maximum reaction distance for any one size of fish at any one time would depend on recognition of the object as potential prey. Recognition of object whose shape and colour is familiar is fundamentally a function of $\emptyset$ min from which it follows that prey diameter and distance combinations resulting in a response angle greater than $\emptyset$ min are either (a) an artefract, as a result of spatial limitations of the

Fig 27. Response angle (ϕ) variation with prey size.

    f in front of resting fish.

    r at maximum distance

    a at maximum reaction field extent.

+ Mean fish length 8.62 cm (June)

O Mean fish length 5.36 cm (August)

● Mean fish length 8.08 cm (September)

Prey Diameter [mean & range] (cm)

apparatus, or (b) the result of some other influence on predatory behaviour.

The maximum r_r value obtained using the 0.875 cm prey (Fig 19) appears to be an artefact, response was sharply cut off within 10 cm of the feed dispenser array, independent of distance from the fish over most of the range, which implies that the true maximum value of r_r could be greater. The points of first reaction fall into three distinct groups. The first of those prey released between 20 and 100 cm on each side of the fish are in a zone where less than half of the prey presented elicited a response. If, as has been suggested, r_r was in fact far greater than 83 cm, then considering the large $\emptyset$ values that would have been subtended with this prey size, a 100% response would have been expected within this zone. As this was not the case, it is likely that fish were recognising some of the prey as unsuitable without needing to involve binocular stereoscopy. The second group of first reaction points were sharply delineated as those of prey released between 10 and 20 cm to each side of the fish, and all were responded to between 30 and 50 cm from the fish. These were presented in the field of view adjacent to the binocular field of the resting fish, and their proximity to the fish (thus potential high net energy gain if acceptable) may have merited scrutiny involving depth perception and thus an absolute evaluation of size. The final group represent prey released within 10 cm of a position directly in front of the fish and would thus have been within the binocular field. Hence fish would have been able to evaluate potential suitability almost immediately on presentation. The reaction occuring within 13 cm of the fish may not have been connected with feeding. Subsequent observation of fish exposed to food particles of this relative size dropped within about 5 cm of fish showed that avoidance or attack behaviour, often accompanied by threat reactions, was the predominant response.

The response to objects that are in excess of 10% of the length

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The response to objects that are in excess of 10% of the length

of the fish (Table VI) and outside the size range that can be ingested (Chapter 3) is unlikely to represent a simple predator-prey reaction. This conclusion is substantiated by the fact that items of this size were never captured (Table III) and usually no response other than head-turn was made.

Consideration of the shape of the field resulting from the 0.435 cm prey, and the distribution of points of first response (Fig 18) shows that: (i) the maximum reaction distance in front of the fish was 44 cm (Cf. maxima figs 16 and 17), (ii) the lateral maximal reaction distance was at least 83 cm. It is likely that the lateral r_r was restricted by the available space within the flume tank, hence the large value of $\emptyset$min that was obtained. A hypothesis accounting for the short, yet apparently spatially non-constrained maximum reaction distance in front of the fish is presented in the second part of this section (p83).

The maximum reaction distance shown by fish exposed to 0.218 and 0.155 cm prey was clearly not affected by spatial constraints (Figs 17 and 16). However r_r in the frontal zone may have been somewhat limited in the case of 0.218 cm prey. A flattening of the frontal part of the reaction field is evident with prey sizes of 0.252 in September and 0.155 in June (Figs 14 and 16) neither of which were likely to have been spatially constrained, so it may be that an upstream deviation from a circular field periphery is characteristic of the reaction field.

Fig 28a shows variation in maximum r_r and r_a corrected for 36% attenuation with prey size. As insufficient experimental data was obtained the value of r_r for 0.109 cm prey was calculated from $\emptyset$min = 10' (p 79) rather than being measured. Extrapolation of the maximum reaction distance and prey size plot obtained for the 0.155 and 0.218 cm prey indicates theoretical values for 0.435 and 0.875 cm prey that may have been obtained in the absence of spatial constraints (Fig 28 a).

In absolute terms fish of 5.36 cm length showed a smaller reaction

Fig 28 (a) Variation with prey diameter of:-

(1) Awareness distance

(2) Maximum reaction distance

(3) Theoretical maximum reaction distance (by
     extrapolation of 0.155 and 0.218 cm point)

(4) Frontal reaction distance

Fig 28 (b) Variation strike field maximum extent with
            prey diameter.

(a)

(1)
(3)
(2)
(4)

Distance (cm)

240
220
200
180
160
140
120
100
80
60
40
20

0·109 0·155 0·218   0·435   0·875
Mean   Prey   Diameter   (cm)

(b)

120
100
80
60
40
20

Distance (cm)

0·109 0·155 0·218   0·435   0·875
Mean   Prey   Diameter   (cm)

field in comparison with 8.62 cm fish. The prey sizes these fish fed on are comparable in relative terms (prey diameter/fish length ratio, Table VI). Thus the reaction field of 5.36 cm fish on 0.185 cm prey can be directly compared with that of 8.62 cm fish on a prey intermediate between 0.218 and 0.435 cm. Reaction distances are expressed in terms of fish body length (bl) it can be shown that the 5.36 cm fish exhibit a larger relative reaction field than the 8.62 cm fish (5.36 cm fish: r_r front = 10.54 bl, r_r maximum = 12.03 bl; 8.62 cm fish: r_r front = 5.83 bl, r_r maximum = 9.63 bl). An increase in the reaction field is a pre-condition of feeding within the increased area necessary if greater relative prey requirements (at uniform prey density) are to be fulfilled. Younger and smaller fish have higher relative food requirements than older and larger fish (Chapter 4) and would therefore be expected to have a larger relative reaction field. Similarly the reduction in the size of the reaction field during September, as compared with June (Cf. 8.08 cm fish on 0.278 cm prey and 8.62 cm fish on 0.218/0.435 cm, Table VI) reflects reduced prey require- ments as a function of lower ambient water temperatures and/or adaptation to winter prey scarcity[*]. This may operate indirectly through reduced awareness distance (see above).

Maximum angle of reaction field.

Due to the spatial limitations imposed by the apparatus it is necessary to resort to some indirect method/comparative reaction field
of

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[*] Unpublished data on seasonal abundance of drift fauna collected by Shackley on the river Bran (Ross-shire) indicate that an abrupt drop in total numbers occurs in September. Minimum total numbers were found to occur in February, and increased proportionally throughout the spring and summer (except for a peak in Chironomid numbers in May) to reach a peak in August representing 7 times the February level. In September total numbers dropped to 3/7 of the August level, then continued to decrease until February.

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relative food requirements than older and larger fish (Chapter 4) and
would therefore be expected to have a larger relative reaction field.
Similarly the reduction in the size of the reaction field during
September, as compared with June (Cf. 8.08 cm fish on 0.258 cm prey and
8.62 cm fish on 0.218/0.435 cm, Table VI) reflects reduced prey require-
ments as a function of lower ambient water temperatures and/or
adaptation to winter prey scarcity[*]. This may operate indirectly
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then continued to decrease until February.

size measurement. The angle subtended at the fish by the outer
periphery of the reaction field (Figs 13, 14 and 16 to 19) is a measure
of the field extent and can be functionally related to response if
recognition is not limited to the binocular visual field. The angle
decreases in the order of subsequent response:

capture/ingest $>$ capture/reject $>$ no capture ...... (Table III)
which reflects the suitability of prey by size. Hence the prey sizes
that were subsequently ingested (0.155 and 0.218 cm) have reaction
field angles of 154 and 156 degrees. A doubling of prey size (to
0.435 cm) reduces this angle by 24 and a further doubling by an
additional 14.

Theoretical relationship between visual field and reaction field.

The reaction field can be divided into an inner zone, in front
of the fish and a peripheral zone, to the sides. Within the inner
zone the maximum reaction distance increases to a maximum at a prey
diameter/fish length ratio (PFR) of 0.025, then decreases rapidly with
further increases in PFR. Response within the peripheral zone is
ambiguous (i.e. fish do not respond to all prey passing through this
zone) and may be directly related to prey size. In the case of a
PFR of 0.0179 inner and peripheral zone reaction distances are similar.
As the PFR increases so the reaction distance in the peripheral zone
increases to a maximum possibly determined by the spatial limitations
of the apparatus.

An hypothesis involving visual field shape can be proposed to
explain the observed results: the visual field comprises a binocular
field subtending 20 degrees of arc, and monocular fields subtending
170 degrees on each side of the fish. It is proposed that a field of
sharp vision, which includes the binocular field, extends to between
40 to 45 degrees on either side of the fish mid-line (i.e. total angle
subtended 80 to 90 degrees)(Fig 29). This follows from consideration of
visual axes direction. Within the binocular field objects can be

Fig 29. Visual field of salmon in the horizontal plane.

Angles in degrees:-

20° - Binocular field

80-90° - Field of sharp vision

190° - Total field of vie of one eye.

Note "visual shadow" to rear of fish.

80-90

20
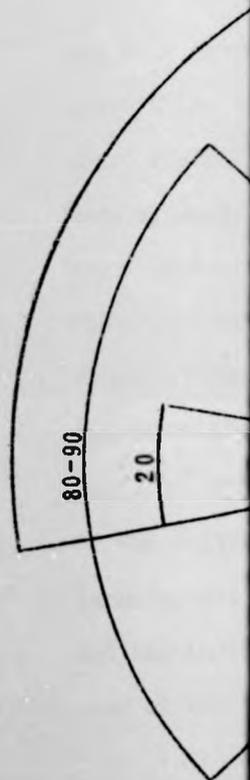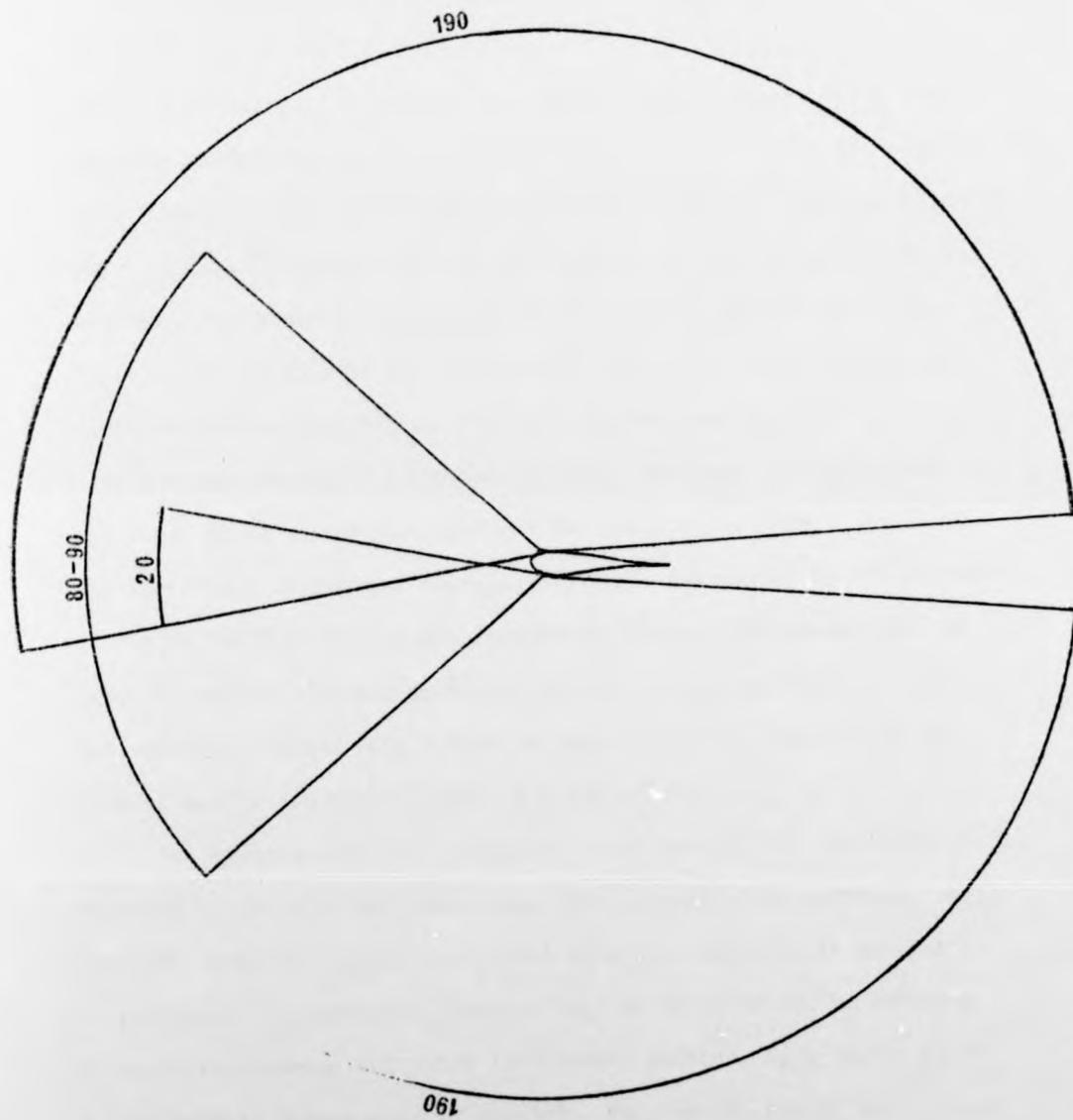
spatially related to each other and the fish, hence a precise measure
of distance, thus object size, can be made. The fish is able to
recognise objects when these are within the field of sharp vision from
cues not involving spatial localisation (by comparison with other
objects, familiarity, etc). Fixation in the binocular field is
required only to confirm recognition and to spatially locate the item
prior to striking. Objects in the field of view outside these zones
can only stimulate awareness in the fish, recognition demands head
orientation towards the object to place it within at least the field of
sharp vision. The inner zone of the reaction field corresponds to the
zone of sharp vision, the peripheral zone to the rest of the visual
field up to the maximum reaction field angle. Variation in reaction
distance between prey of the same size in the same zone occurs as a
result of the mechanics of accommodation. Each eye can only focus on
one depth plane at any one time and the smaller the object the less
the likelihood of retinal stimulation (hence awareness) as the distance
of the object from this plane increases. This would account for the
large spread of reaction distances with the 0.155 and 0.218 cm prey,
and the localisation into a band of points of first response in the
case of the larger prey (0.435 and 0.875 cm).

An expansion of this hypothesis would account for the decrease in
reaction distance in the inner zone with prey diameter increase, while
reaction distances in the peripheral zone increase. It is necessary
to postulate a recognition distance (r_d) which would not be betrayed
by an overt response and which is directly related, by a factor K, to
a (the angular measurement of acuity). Thus within the field of sharp
vision preliminary recognition takes place at:

$$r_d = K\frac{L}{\tan \underline{a}} \qquad \text{(see equation 1)} \ldots\ldots\ldots\ldots(3)$$

but is betrayed only when final localisation, prior to some response
taking place, occurs (i.e. at r_r, equation 2). Therefore the reaction

Fig. 30.   Theoretical relationship between visual field and
reaction field.

REACTION FIELD

VISUAL FIELD

AWARENESS

FIELD OF SHARPEST VISION

BINOCULAR FIELD
(10°)

FIELD OF SHARPEST VISION
(1.0-4.5°)

Fig. 30.   Theoretical relationship between visual field and

reaction field.

REACTION FIELD

VISUAL FIELD

AWARENESS

FIELD OF SHARPEST VISION

BINOCULAR
FIELD
(10°)

FIELD OF (40-45°)

VISUAL FIELD

REACTION FIELD

AWARENESS

FIELD OF SHARPEST VISION (4.0-4.5°)

AWARENESS

BINOCULAR FIELD (10°)

RECOGNITION AND SPATIAL LOCALISATION

RECOGNITION

MONOCULAR FIELD 170°

REACTION FUNCTION OF DECISION TO STRIKE

REACTION DEPENDS ON DECISION TO CONFIRM RECOGNITION BY BINOCULAR STEREOSCOPY

RECOGNITION DEPENDS ON REACTION BY HEAD (REACTION FIELD=RECOGNITION FIELD)

REORIENTATION

MAXIMUM EXTENT OF REACTION FIELD

VISUAL SHADOW
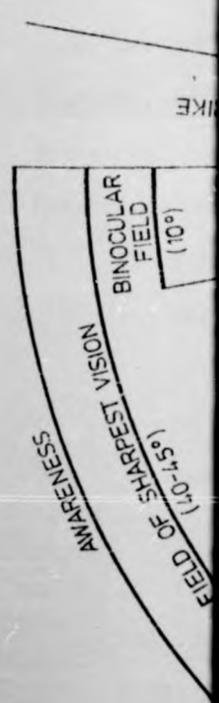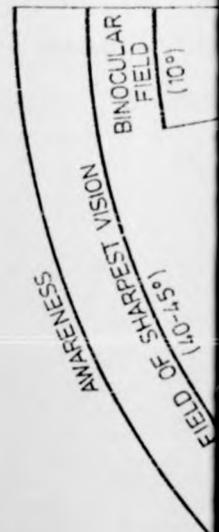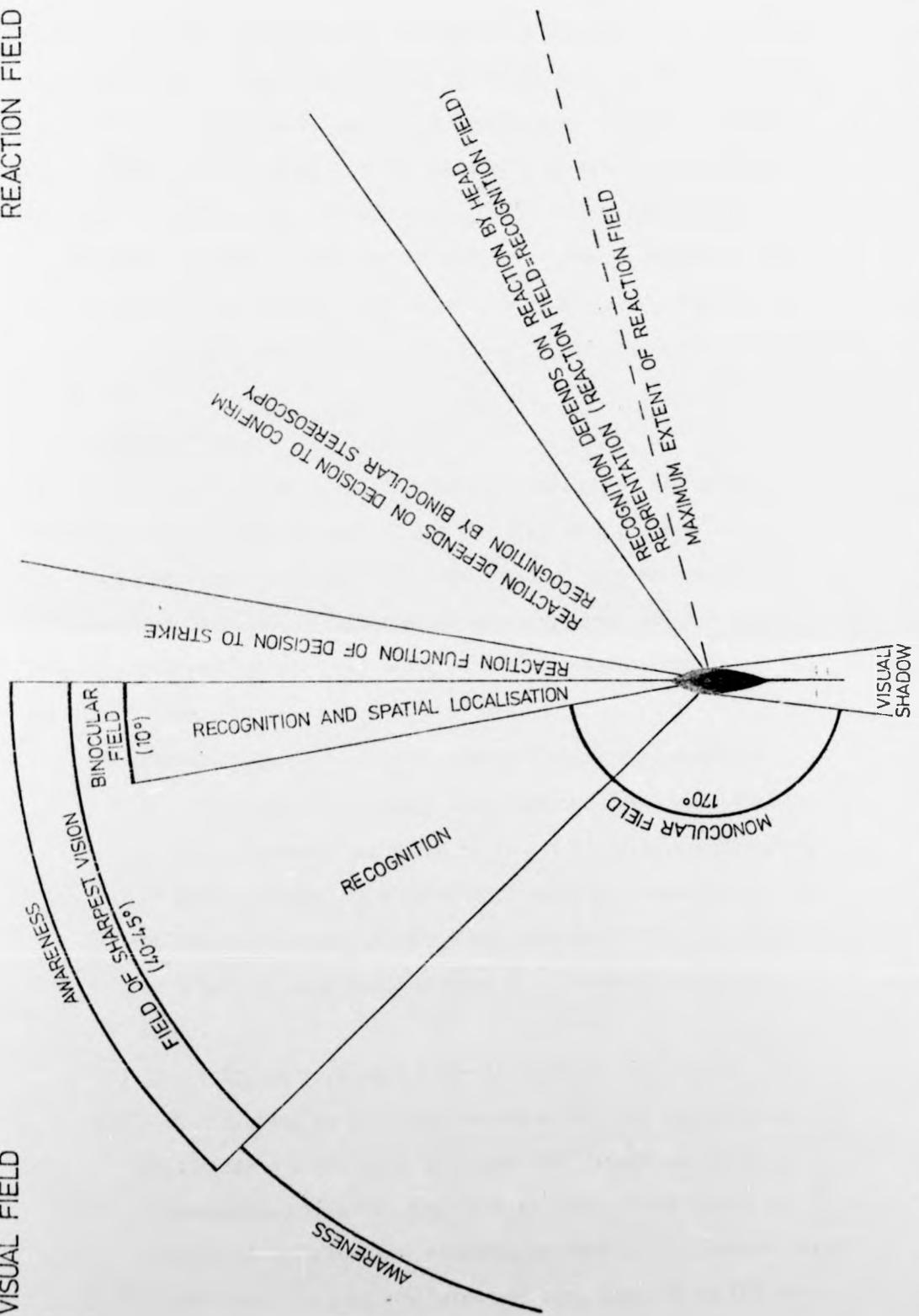
distance, _per se_, is independant of $\emptyset$min in the inner zone. In the peripheral zone recognition requires orientation of the field of sharp vision towards the object, thus r_d is betrayed by an overt reaction. Hence in this zone $r_d = r_r$ and the reaction distance is a function of $\emptyset$min, and therefore, by extension, _a_. The line of extrapolation (3, Fig 28) therefore represents recognition distance variation with object size in both the inner and peripheral zones as well as reaction distance in the peripheral zone. The foregoing hypothesis is summarised in Fig 30.

Striking Field.

The effect of prey size, fish size and season on the strike field is obvious from Tables II and III and Fig 28b. The linear extent (i.e. maximum strike distance) was a function of maximum reaction distance, and prey, when responded to, were captured with the same frequency independant of their position in the reaction field. Exceptions were:

I) Striking at 0.109 cm prey only took place when reaction distances were far shorter than maximum. From observations striking distance was found to be 1.5 bl (i.e. approximately 13 cm)as compared to a calculated reaction distance of 38 cm. The poor economics of energy expenditure involved in capture of this prey size would account for the restricted strike field.

II) The 0.875 cm prey were never captured.

III) Fish feeding in September showed a very reduced striking field (Fig 14, Table II) compared with August and with corresponding relative prey size in June. This result is consistent with low prey requirements due to low ambient water temperatures, and/or adaptation to prey scarcity (p 82) at this time of year.

The relationships between striking   and prey size are a

function of the mechanics of feeding and will be given some further

consideration in Chapter 3.

CONCLUSIONS

The calculated maximum distance of awareness of fish 8.62 cm in length, corrected for optical attenuation within the water, varied with prey size from 0.48 m (prey diameter 0.109 cm) to 2.20 m (prey diameter 0.875 cm).

The reaction field varied directly with prey size up to a maximum prey diameter/fish length ratio (PFR) of 0.025 (i.e. 0.218 cm prey, 8.62 cm fish). With increasing PFRs above this value the reaction field progressively decreased (PFR range 0.013 to 0.102).

Reaction field decreased (i) with reduced fish size, and (ii) between June and September, corresponding to a seasonal ambient water temperature drop from 17 to 10°C, by a factor of about 4 (all at comparable PFRs).

The mean minimum angle subtended by prey at the eye of the fish that elicited a response was 10'. Reaction distance was found to be independant of this angle. A hypothetical recognition distance is proposed to account for discrepancies between awareness and reaction distances in different parts of the visual field.

Prey size resulting in a PFR of 0.102 (i.e. 0.875 cm diameter) was found to elicit responses that were not characteristic of predation. No prey of this size was ever captured. It is proposed that over a threshold PFR objects of characteristic prey colour and shape are not treated as prey.

Prey of PFR 0.051 (i.e. 0.435 cm diameter) were predominantly captured, and subsequently rejected. Prey of PFR 0.025 and 0.018 were captured and ingested.

Striking distance varied directly with reaction field size (i.e. maximum at PFR 0.025) with the exception of prey of PFR 0.102.

It is concluded that (i) awareness is a function of the entire visual field, (ii) recognition initially depends on fixation in the frontal field of sharpest vision, and (iii) spatial localisation and

precise evaluation of size depends on fixation in the binocular field. It is proposed that the angle subtended by each part of the visual field from the fish mid-line is (i) entire field: 180 degrees, and (ii) frontal field: 40 to 45 degrees (iii) binocular field: 10 degrees and hence (iv) monocular field: 170 degrees.

CHAPTER 3

The Feeding Mechanism and Prey Size Selection

Contents:

GENERAL INTRODUCTION

A) THE MECHANICS OF PREY CAPTURE, INGESTION AND EJECTION.

   The functional morphology of the head

   Prey capture

   Manipulation within the buccal cavity

   Ejection of prey and coughing

   Ingestion of prey

SUMMARY

B) PREY SIZE SELECTION

   Introduction

   Physical limitations on prey size

        Mouth breadth

        Branchial basket structure

   Physiological influences

   Behavioural influences

CONCLUDING COMMENTS

GENERAL INTRODUCTION

Initially prey size selection occurs purely due to limitations in perception imposed by the visual system of the fish and its optical environment (i.e. increase in distance of recognition with increase in prey size). Visual constraints impose themselves on the distance of reaction to different prey sizes, essentially increasing the accessibility of larger items as compared with smaller ones as the size of the reaction field increases. However it is clear that with increase in prey size past an optimum diameter the reaction field is modified, prey are captured then subsequently rejected, then finally the strike itself is suppressed as prey pass a threshold size (Chapter 2). In the case of a predator that ingests its prey whole minimum and maximum prey sizes must exist which relect its handling capabilities. As a first approximation these limits can be assumed to be a function of the mechanics of capture and ingestion. It is therefore pertinent to examine such limitations in the light of the acceptance and rejection behaviour exhibited by the fish during the experiments reported in Chapter 2.

This Chapter is therefore primarily concerned with post-reaction selectivity. As this is directly dependent on capture behaviour, and as physical limitations on suitable prey size operate through the ingestion mechanism, a functional description of this behaviour forms the main part of the chapter. This is followed by the result of morphometric measurements of the parts of the feeding mechanism directly relevant to selectivity, and further consideration of acceptance - rejection behaviour on different sizes of prey.

(A) THE MECHANICS OF PREY CAPTURE, INGESTION AND EJECTION

The strike and associated activity culminate ideally in successful capture and ingestion of the prey. In all but one out of 68 strikes studied in the flume tank experiments (Chapter 2, excluding the 0.800 to 0.950 cm prey size) fish captured the prey. Subsequent treatment, however, depended almost entirely on the size of the prey (Chapter 2, Table III) and comprised either ingestion or ejection of the prey after it had been taken into the buccal cavity. The entire sequence can therefore be divided into three clear phases:-

(i)   capture, and intake into the buccal cavity

(ii) manipulation within the buccal cavity

(iii) subsequent ejection from the buccal cavity, or

      ingestion of prey into the digestive tract proper.

Occasionally fish would eject then re-capture particularly troublesome prey, although in many cases subsequent total rejection occurred. Ingestion presumably involves a swallowing action involving oesophageal and associated musculature activity which can only be investigated using EMG recordings or similar techniques. Details of this activity were not investigated and no published information is known to the author. Presumably the purpose of manipulation prior to possible ingestion is to position the prey such that swallowing can take place, although attempted breaking up of the prey is a possibility. As some break up of prey does appear to occur in many instances ejective behaviour must be considered to serve at least two purposes, namely the spitting out of unsuitable prey and the clearing of gill structures of small break up products by

means of the classic cough sequence. The latter follows from the pro-
nounced respiratory movements, described below, that occur during feeding
and result in the passage of material across the gills.

The functional morphology of the head

The information presented in this section is based entirely on
Ballintijn (1969, 1 and 2), Ballintijn and Hughes (1965), and Osse (1969),*
who described the head morphology of trout.

Fig. 1 is a schematic diagram showing the skeletal structures of
the head, much simplified, and the respiratory and feeding musculature.
The branchial arches (carrying the gill lamellae) stretch between the
neurocranium and the ventral element of the hyoid. The muscles of the
head shown are active during respiration, coughing, and feeding and fall
into two groups, those that expand and those that reduce the volume of
the buccal and opercular cavities. The buccal cavity is sealed from the
mouth side by the action of one-way flap valves when the mouth is closed
(lower jaw adducted), and from the opercular side by adduction of the
branchial arches, thereby sealing <u>via</u> the gill lamellae. In addition
the buccal cavity connects to the oesophagus <u>via</u> a sphincter. The oper-
cular cavity seals along the posterior edge of the operculum when this
is lying close to the body by means of the opercular flap valve which is
also one-way in action. Sealing at this point persists after the
beginning of abduction of the operculum and can occur while adduction
is still taking place. Thus by movement of the operculum a negative or
positive pressure can be induced in the opercular cavity relative to the
buccal. Normal respiration occurs by the sequential expansion and con-

---

* The structure of the head of Atlantic salmon is essentially similar
to that of trout. Dissection of salmon and comparison with trout con-
firmed this view, as did Alexander (1967).

Fig. 1   Skeletal and muscular structure of the head, lateral
           and ventral views.

           Legend: **nc** neurocranium

                pm   premaxilla

                max   maxilla

                lj   lower jaw

              pal pt Palato-pterygoid

                qu   quadrate

                hmd   hyomandibula

                op   operculum

                sth   stylohyal

                hy   hyoid

                cl   cleithrum

               br r   branchiostegal rays

           ADD APO **adductor arcus palatini et operculi**

              STHY   sternohyoideus

           LEV HAP levator hyomandibula et arcus palatini

              D O   dilator operculi

           ADD M   adductor mandibulae

             HY HY   hyohyoideus

              P HY   protractor hyoideus

               ^^   ligaments

           (Redrawn, with additions, from Ballintijn and Hughes, 1965)
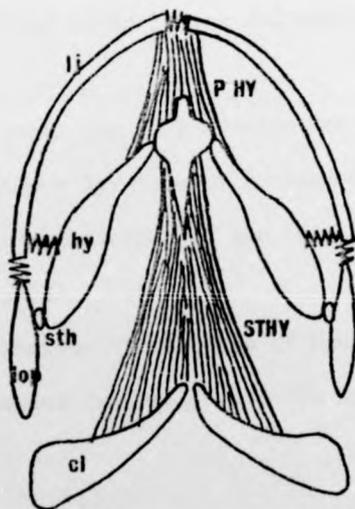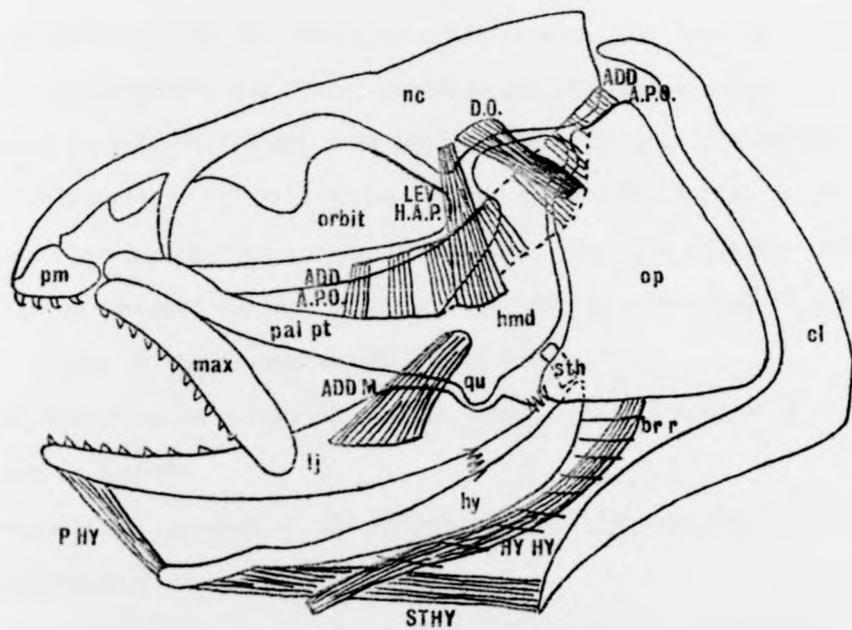
traction of the buccal and opercular cavities such that they act as an opercular suction pump and buccal pressure pump (Hughes and Shelton, 1958). The result is a flow of water over the gill lamellae from the buccal to the opercular side. The gill arches can be extensively raised to permit unimpeded flow during respiration and feeding. The flow of water across the gills is reversed during coughing apparently by a reversal of the mode of action of the opercular and buccal pumps.

The following is a list of muscles shown in Fig. 1 and their functions in trout*:

Dorso-caudal element of the <u>adductor a.p.o.</u> (<u>Levator operculi</u> equivalent):

Levation of the operculum which swings on its articulation with the hyomandibula, thus the ventral component of the opercular complex moves dorsocaudally, and, <u>via</u> the mandibular-opercular ligament the lower jaw is abducted.

<u>Sternohyoideus</u>:

(i) Abduction of lower jaw as a consequence of hyoid depression, hyoid retraction (hence levation of operculum due to articulation with the hyoid), and stretching of the skin.

(ii) Expansion of palatal complex.

(iii) Increase in cross-sectional area of mouth as the inner ends of the lower jaw expand laterally with the hyomandibula and palatal complex.

---

* Due to specialisations in feeding and adaptations to respiratory environments, other fishes, such as carp and perch, show a far more complex musculature, differentiated into individual muscles rather than muscle sheets, and a corresponding variation in function. The musculature and head morphology can be adapted for suction (e.g. perch), scooping/suction (e.g. carp), and biting (e.g. trout) feeding modes. As this aspect of feeding is identical in salmon and trout direct comparisons can be drawn.

(iv) Abduction of branchial arches due to hyoid retraction.

(v) Expansion of the operculum, due to hyoid and hyomandibular expansion as a consequence of opercular-hyomandibula articulation.

Levator hyomandibula et arcus palatini:

Abduction of operculum, lateral expansion of the lower jaw and hyoid as a result of palatal complex expansion, and abduction of branchial arches as a result of hyoid expansion.

Dilator operculi:

Opercular abduction.

Adductor mandibulae:

Adducts lower jaw, as a consequence of which the hyoid is raised hence hyomandibula the operculum adduct.

Hyohyoideus:

Adducts branchial arches and helps in opercular adduction.

Ventro-rostral element of adductor a.p.o.:

Adduction of hyomandibula, thus branchial arch adduction.

Protractor hyoideus:

Raises hyoid, then branchial arch adduction follows.

It can therefore be seen that the complexity of couplings results in interdependence of movement between elements, often those far removed from the initiator.

Prey capture - Plates 1, 2 and 3.

As the mouth commences to open so the floor of the buccal cavity is depressed as a consequence of hyoid depression and expands laterally as the palatal complex and operculum expand. A secondary consequence of these movements is the expansion of both the branchiostegal apparatus and branchial basket complex as the branchial arches abduct. Thus both buccal and opercular cavity volumes are greatly increased allowing an element of suction to enter what is predomina ntly a snapping feeding mode (Plate 1c). The expansion of the branchial basket results in the appearance of gaps between adjacent hemibranchs which can clearly be seen in Plates 2 (arrowed) and 8(g). Of particular interest is the sudden extreme opercular abduction clearly visible in Plate 3. This is characteristic of all prey captures by salmon irrespective of prey size and occurs to an apparently reduced extent in the trout. Gill arch raising is a consistent feature of opercular abduction and is accompanied by activity in the gill lamellae musculature (Young, 1972), hence permitting free flow of water through the system. The buccal cavity floor is raised and the cavity volume decreases immediately after the mouth is closed. Water contained in the buccal cavity flows across the branchial basket and out through the opercular valve immediately before the operculum adducts completely. Therefore small particulate material contained within the mouth may be carried with this water and out by the opercular aperture.
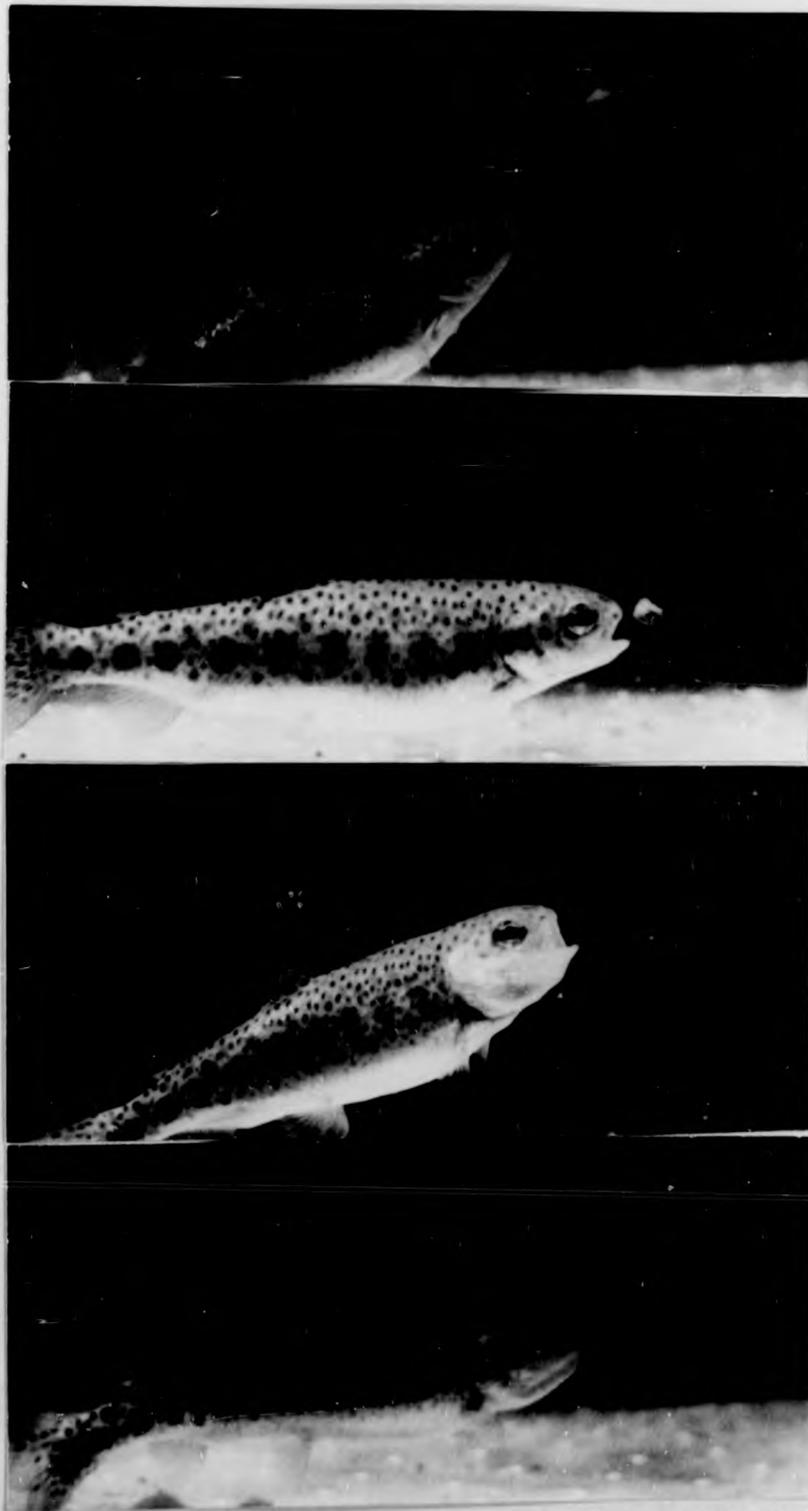
Plate 1 Rainbow trout capturing food particle. Shots a to d not from same sequence, approximate duration 0.5 sec. Static water conditions.

Plate 2 Rainbow trout during yawn, note expanded buccal cavity and
pronounced apertures between gill arches traversed by gill
rakers.

Plate 3 (a and b).   Atlantic salmon capturing prey.

Total duration of sequences 0.30 sec. Feeding under current

of approximately 18 cm sec^{-1}, direction arrowed.

3a. Note prey entering mouth in frame c, then opercular and

branchiostegal ray expansion in following frame (d).

3b. Note wide mouth opening as prey is captured (frame e)

followed immediately by extreme opercular expansion

(frame f) then adduction (frame g).
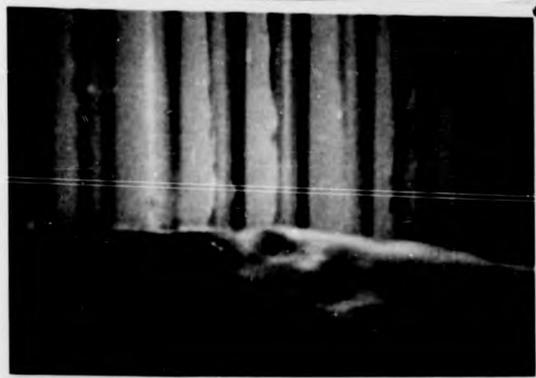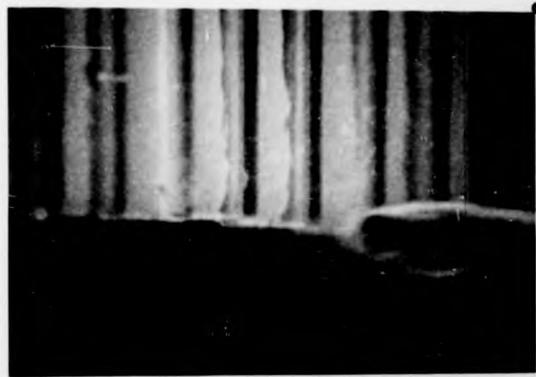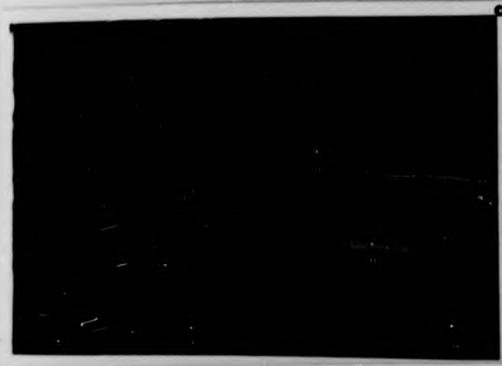
Manipulation within the buccal cavity - Plates 4, 5 and 6.

Immediately following mouth adduction on the intake of prey into
the buccal cavity there occurs a series of rapid jaw movements. These
occur at a frequency of about 0.33 sec and are a consequence of relaxa-
tion and contraction of the adductor mandibulae muscles (Oswald, 1977,
MS). Overall amplitude of movement is less than that of the initial
abduction but both buccal cavity volume changes and opercular abduction
occur (Plate 4). Plates 5 and 6 show the extent of opercular abduction
in trout during prey manipulation, and small particulate break up pro-
ducts (arrowed) can be seen being voided via the opercular valve in
Plate 5. The total period of time taken for manipulation varies between
1 and 3 sec, after which ejection occurs if prey is not ingested.
During this time opercular and buccal volume changes presumably enable
gill ventilation to continue, the loss of small particles through the
gill slits being a necessary penalty of continued respiration during
this violent activity. Respiratory musculature activity increases to a
level similar to that seen during heavy respiration (Hughes and Roberts,
1970), at which level rhythmic gill slit opening has been demonstrated
by Saunders (1961).

Ejection of prey and coughing - Plates 7 and 8

The cough is a reversal of flow over the gills which may result in
ejection of water through the mouth. It is an interpolation within the
normal respiratory cycle of an expansion of both cavities followed by a
contraction. Four stages of intensity have been identified: (i) Weak
cough; synchronous expansion of both cavities accompanied by little

Plate 4.   Atlantic salmon feeding, showing buccal manipula-

tion of prey following capture.

Filmed at 24 f.p.s., total duration of sequence 0.5 sec.

Feeding water current approximately 18 cm sec^{-1}, direction

arrowed.

Note:-   frame b, opercular expansion
            c, lower jaw abducted
            d, lower jaw raised

            j, lower jaw abducted, mouth open
            k, lower jaw abducted, mouth closed,
                operculum expanded
            l, lower jaw raised
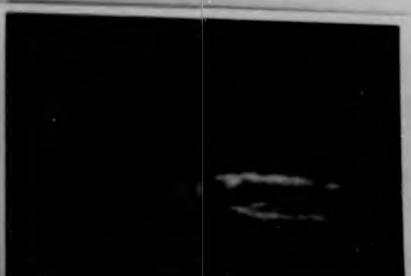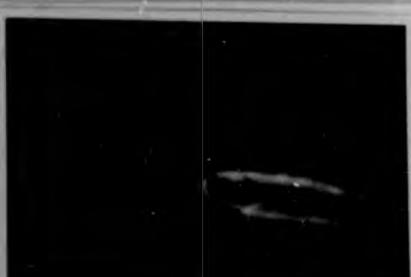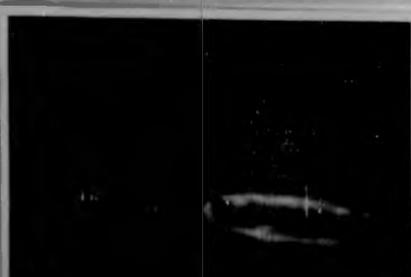
Plate 5.   Rainbow trout immediately post capture, showing abducted
opercula during buccal manipulation of prey. Note fine material
voided via opercular apertures (arrowed).

Plate 6.   Rainbow trout immediately post capture, showing abducted
operculum during manipulation of prey in buccal cavity.

Plate 7.   Rainbow trout ejecting prey.

Frames taken at 0.23 sec intervals, static water conditions. Note
intense opercular and branchiostegal abduction in frame c, followed
by rapid adduction and prey ejection by the following frame.

Plate 8.   Rainbow trout ejecting prey.

Frames taken at 0.23 sec intervals, static water conditions.

Order of frames in sequence:

<div style="text-align:center">

a   b

c   d

e   f

g   h

</div>

Note series of opercular abductions-adductions preceding

slow opening of mouth then ejection of prey.   Branchial arch

apertures are clearly visible in frame g.
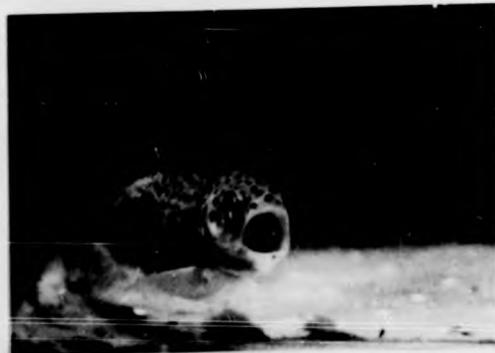
ns .

rch

change in pressure (Hughes, 1975). (ii) Intense cough; involving a high pressure change in the buccal cavity, opercular and branchial arch abduction, hence sudden reversal of flow across the gill lamellae (Hughes, 1975). (iii) Spitting; which involves ejection of buccal contents and water through the mouth (Ballintijn, 1969, 1). (iv) Yawn or gasp; characterised by marked opercular abduction and exaggerated lowering of the jaw (Hughes, 1975). All involve reversal of flow between the gill arches. The weak cough is likely to be a stress-induced displacement activity (Osse, 1969) while the more intense cough is a mechanism for clearing the gills of irritant material (Ballintijn, 1969; Osse, 1969 and Hughes, 1975). A mechanical stimulus is necessary both for intensive coughing and the violent cough/buccal contents ejection termed spitting (Young, 1971).

Violent ejection of prey from the buccal cavity characterised feeding in both the trout and salmon, but in salmon was predominantly found in prey that was subsequently totally rejected. The duration of the spit was similar to that reported by Hughes (1975) for intense coughing, i.e. less than 0.33 sec. A fish experiencing difficulty with a prey item would violently abduct the opercula and expand the branchiostegal apparatus. In most cases opercular adduction was closely followed by buccal cavity volume contraction, hence ejection (Plate 7) although in some cases the protracted sequence shown in Plate 8 took place.

Ingestion of prey - Plate 9.

Plate 9 illustrates final intense abduction of the lower jaw and operculum as ingestion takes place. Following this normal respiratory

Plate 9.   Head movements of salmon as prey is ingested.

Filmed at 24 f.p.s., total duration opercular and jaw move-
ments 0.1 sec. Note extreme opercular expansion and upper
jaw retraction in frame f as prey is ingested. Fish showed
no feeding movements subsequent to frame f.

a	e
b	f
c	g
d	h

move-
per
owed

movements continue without the rhythmic jaw movements characteristic of prey manipulation. Although the prey size in this case was quite small (about 0.20 cm in diameter, see Plate 3b) raising of the upper jaw can be seen to be prominent, and expansion is more pronounced than at capture. Such an intensity was not characteristic of all ingestions although pronounced movement always occurred.

SUMMARY

1)   Prey intake is a combination of snapping and active suction into the buccal cavity and involves sudden and extensive abduction of the lower jaw, gill arches, and operculum, then rapid adduction in that order. Small particulate material taken in through the mouth may be voided via the inter-gill arch apertures.

2)   Prey manipulation within the buccal cavity involves a series of slightly lower amplitude jaw, gill arch and opercular abductions-adductions occurring at a frequency of approximately 0.33 sec over a period of 1 to 3 sec. Again fine material may be voided through the gills.

3)   Unsuitable prey and fine material irritating the gills are voided through the mouth by the reversal of water flow through the opercular and buccal cavities. The complete ejection sequence may take place in less than 0.33 sec.

4)   Ingestion of prey is accompanied by extensive jaw and opercular abduction, similar to that occurring during prey manipulation.

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(B) PREY SIZE SELECTION

Introduction

The evidence for prey-size selection in teleost fish, and particu-
larly in salmonids, is overwhelming. Broadly speaking this evidence
falls into two categories, namely that obtained from the wild by compari-
son of fish stomach contents with the size distribution of potential prey
in the environment, and electivity or preference experiments involving
predator and/or prey manipulations.

Correlations between fish size and prey size have been found in
several fish species (LeCren, 1958; Parsons, 1971 and Wong and Ward,
1972) including char (Salvelinus spp) (Martin, 1952; Lindström, 1956 and
Moore and Moore, 1974), coho salmon (Zorbidi, 1973), coregonids (Nilsson,
1957 & 1958), rainbow trout (Ricker, 1930 and Metz, 1973) and Atlantic
salmon (Allen, 1941). Additionally, experiments involving confined
predator and prey populations have shown similar results (LeBrasseur,
1969; Hall, Cooper and Warner, 1970). Depending on fish species and
geographical location three classes of response have been demonstrated.
Brooks (1968) sampling a range of planktivorous fish species, and
Zorbidi (1973), working on coho salmon, report a selection biased towards
the largest available prey. Conversely, Gerking (1972), Beyerle and
Williams (1968), working on sunfish (Lepomis spp) and northern pike
(Esox lucius) respectively, and Feller and Kaczynski (1975) on chum
salmon (Onchorhynchus keta), all found strong selectivity for the
smallest prey individuals found in the prey population. The third type
of response has been demonstrated in brook trout, chum and pink salmon,
and Atlantic salmon and brown trout by Allen and Clausen (1960), Okada

and Taniguchi (1971), and Egglishaw (1967), respectively, who found an increase in the size range of prey with increase in predator size.

In most of the above cited examples severe sources of error were present (Gerking, 1962 and Egglishaw, 1967), and only limited speculation can be made as to the causative factors underlying the observed size distribution of stomach contents. For example Werner and Hall (1974) have shown that sunfish select larger prey as prey density increases, and Ivlev (1961) found that selection was strongly influenced by prey abundance and the degree of concentration (i.e. distribution).

Behavioural experiments aimed at determining predator preferences for particular prey and prey parameters have been conducted on various fish species. Ivlev (1961) found that predatory fish (e.g. pike, roach) preferred the largest possible prey that they could handle, benthophagic fish (e.g. carp, bream) showed equal avoidance of larger and smaller than optimum prey, and planktivorous fish (e.g. bleak) showed greater selectivity for smaller rather than larger than optimum prey. Strong preference for objects of a particular size or size range has been demonstrated in minnows (Zunini, 1937), perch (Boulet, 1960), and several other teleosts (Protasov, 1968). Labass (1959) has shown that 0+ salmon showed a strong preference for objects in the length range 0.07 to 0.09 of their body length.

Both physical and physiological factors can be postulated as placing possible limitations on the size range of material that can be handled satisfactorily. The behaviour of the predator will thus in part have developed on the basis of these limitations but will also depend on other aspects which either indirectly determine selection (e.g. visual

acuity) or influence the motivational state of the animal (e.g. hunger).

Physical limitations on prey size

The maximum gape of the mouth will obviously place a limit on the size of whole prey that can be ingested. Growth of the fish therefore extends this maximal prey size limit. The minimum dimension of the mouth at maximum gape will clearly constitute the limiting factor. Laurence (1958), studying largemouth bass, Yasuda (1960), four species of predatory marine fish, and Okada and Tanigushi (1971), working on pink and chum salmon found that the maximum breadth of the prey animal corresponded closely with predator mouth breadth. Prey breadth was found to be of critical importance as the fish under consideration manipulated prey until the longitudinal axes of predator and prey were coincident before swallowing. Similarly Northcote (1954) found that the mouth gape to length relationship of two species of Cottus corresponded with observed diet differences. Wong and Ward (1972) demonstrated a relationship between mouth gape and prey size during the short phase within which yellow perch fry showed size selective predation on Daphnia, and Werner (1974) showed a mouth gape/prey size relationship in two species of sunfish.

Nilsson (1958 & 1965) found a rough correspondence between the number of gillrakers on the branchial arches of coregonids and prey size, and Werner and Hall (1976) considered that gillraker length and spacing in part determined foraging patterns in three congeneric species of sunfish. The structure of the branchial basket (comprising branchial arches, gill rakers, spines and teeth) has been proposed as a limiting factor that determines the minimum threshold size of prey for several

planktivorous fish species (Ivlev, 1961 and Lauzanne, 1970) and for two
species of tuna (Nakamura, 1968). A direct relationship between minimum
prey size and the structure of the branchial basket has been demonstrated
in bathypelagic fish by Ebeling and Caillet (1974). Conversely Galbraith
(1967) concluded that the abrupt lower prey size threshold that he found
in rainbow trout was not related to gill raker spacing, but was due to
selection of individual prey. In view of the fact that small particulate
material is voided through the opercular apertures during feeding (p. 98)
it is suggested that the size distribution of this material would depend
entirely on the filtration efficiency of the branchial basket structure
as a whole. Gill rakers and associated spines and teeth, if these are
present, would exert the strongest influence provided they traversed the
inter-hemibranch spaces fully.

Mouth breadth. Observations of salmon and trout feeding show that at
maximum gape (e.g. Plate 8g) the dorso-ventral dimension of the mouth
is approximately 50% greater than the breadth (the maximal internal
side to side dimension, measured between the inner ventral edges of
the maxillaries). On freshly-killed specimens this was found to
correspond to the maximum mouth opening that could be forced without
damaging the muscle tissues. Measurements of mouth breadth,
dorso-ventral opening, and angle between upper and lower jaws
(measured from the innermost point in the jaw angle and not the
maxillary-lower jaw intersection as these structures become slightly
separated at maximum opening) on several fish showed that breadth
increases only very slightly with angle of opening. For example

Fig. 2.   Mouth breadth variation with fish length.

      E -   External breadth ($r = 0.990$, $P < 0.001$)

      I -   Internal breadth ($r = 0.994$, $P < 0.001$)
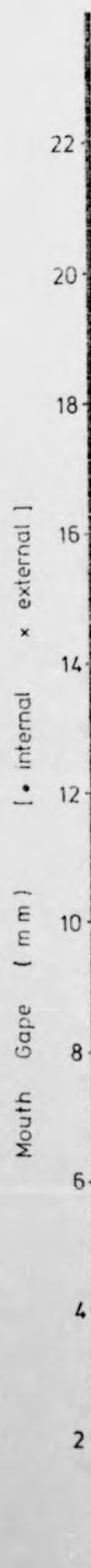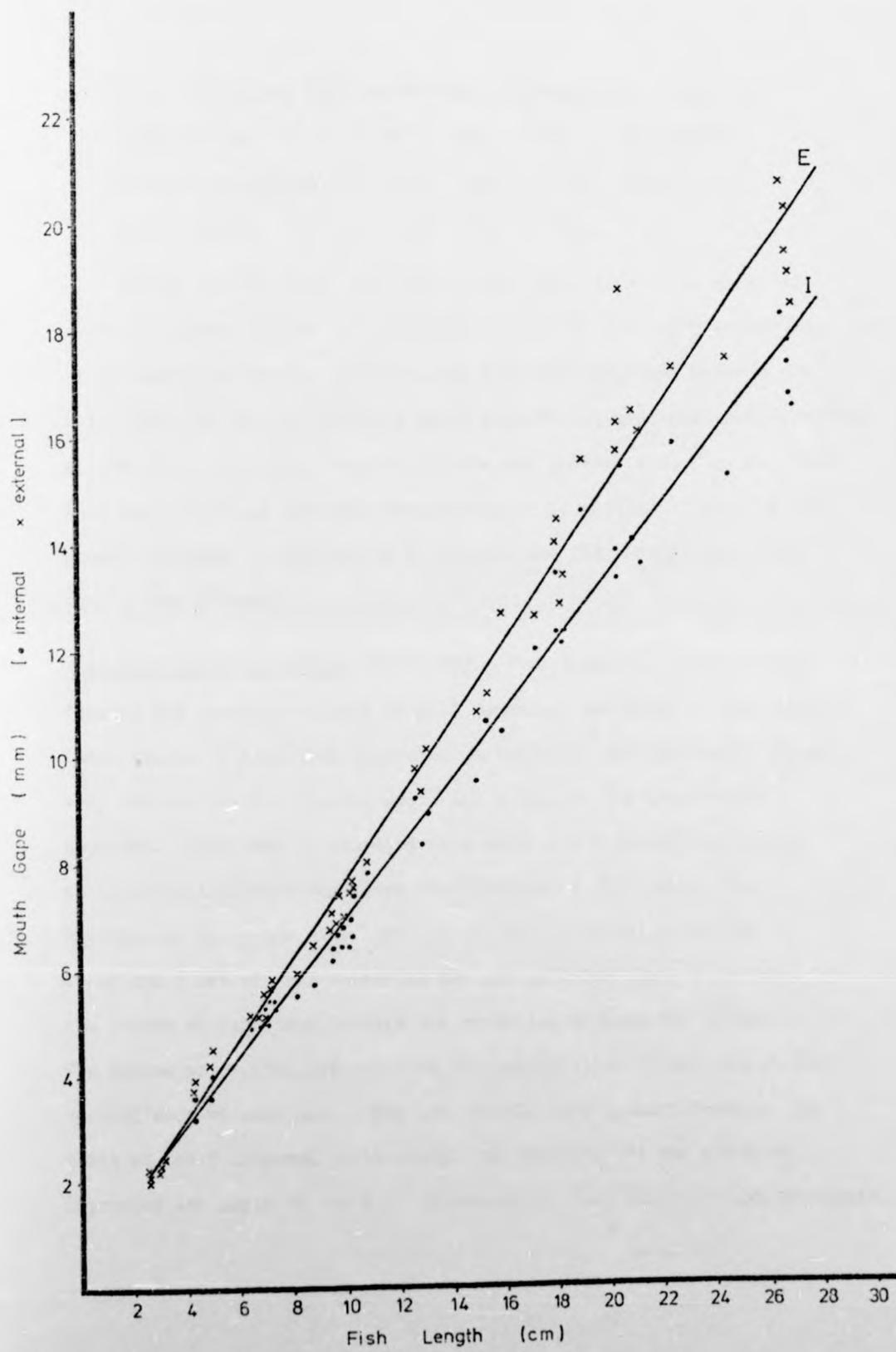
a fish of fork length 15.0 cm had the following mouth dimensions:

angle of jaw	-	30	60	160	(degrees)
dorso-ventral diam.	-	5.0	10.0	16.3	(mm)
mouth breadth	-	9.2	9.8	10.5	(mm)

During capture trout and salmon open their jaws to an angle of about 60 degrees (Plate 1c) at which opening the two major dimensions of the mouth are equal. Internal and external (measured between the outer edges of the maxillaries) mouth breadth was measured in 56 freshly-killed juvenile salmon, and the results are presented in Fig. 2. Fish were sacrificed and examined immediately on completion of each of the growth experiments reported in Chapter 4, one fish being taken from each of the 6 tanks.

Branchial basket structure (Plate 10). Five branchial arches, each forming the posterior margin of gill aperture, are found in the salmon. Total length of each arch decreases posteriorly, the fifth arch being very reduced and forming the posterior margin of the respiratory appartus. Each arch is composed of a ventral and dorsal hemibranch which articulate slightly above the mid-line of each arch. The hemibranchs carry the gill lamellae on their external posterior faces and a set of gill rakers on the mid-anterior face, such that the rakers of each arch overlie the preceding arch on the inside. The degree of overlap reduces from the articulation to the dorsal and ventral ends of each arch. The hemibranchs form a sharp V-shape, the point of the V directed posteriorly. As the floor of the mouth is depressed the angle of the V is increased and gill raker overlap decreases.

Plate 10.   Branchial Basket Structure - Salmon.

   a)   Head, showing operculum and branchiostegal apparatus.

   b)   Operculum and left lower jaw removed. Note gill
        lamellae overlying each other, and rakers on first arch.

   c)   As 'b', arches abducted and pulled rostrally.

   d)   Left-hand gill arches removed, showing internal branchial
        basket structure on right-hand side of head. Note over-
        lying rakers traversing preceding arch in each case, and
        length decrease dorsally and ventrally along each arch.

hial

er-

and

n.

a

b
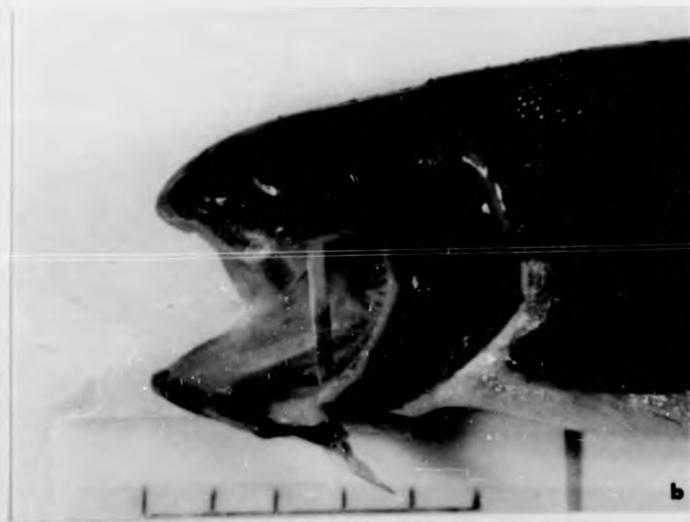
However as movement is maximal at the hemibranch articulation where raker overlap is also maximal the rakers do not cease to overlie the preceding arch at any point. At maximum depression, at which point each arch is almost straight, rakers still traverse each gill aperture. During feeding the branchial arches are expanded outwards as well as abducted forwards. Lifting the arches together and pulling them rostrally to simulate this feeding movement similarly does not prevent raker overlap.

No spines or other ancillary structures can be seen, although in larger specimens (20 cm +) the external face of each hemibranch bears a row of small 'teeth'. The first branchial arch carries in excess of 24 rakers in all cases, the number being progressively reduced until the fifth arch carries only about 10.

Raker length is maximal at the hemibranch articulation and decreases towards the dorsal and ventral ends of the branchial arch. Similarly the distance between adjacent rakers decreases along each hemibranch although not to the same extent as the length. The width of the gill aperture is maximal at the hemibranch articulation and decreases to zero towards the ends of each arch. This occurs as a consequence of the V-shape and also due to hemibranch width increase dorsally and ventrally. Gill lamellae size increases towards the point of the V. It can be concluded that maximum gill aperture and lamellae size indicate a region of maximal water flow and that therefore most suspended material passes through the gills in the central part of each gill aperture. It is therefore clear that the rakers can constitute an effective filtration device which would act as a screen inhibiting the voiding of particulate material through the gill apertures.

Fig. 3.   Gill raker length (gill arches 1 to 5) variation with

fish length.

Arch	r	P
1	0.9882	<0.001
2	0.9896	<0.001
3	0.9817	<0.001
4	0.9752	<0.001
5	0.8637	<0.001

Gill Raker Length (mm) vs Fish Length (cm)
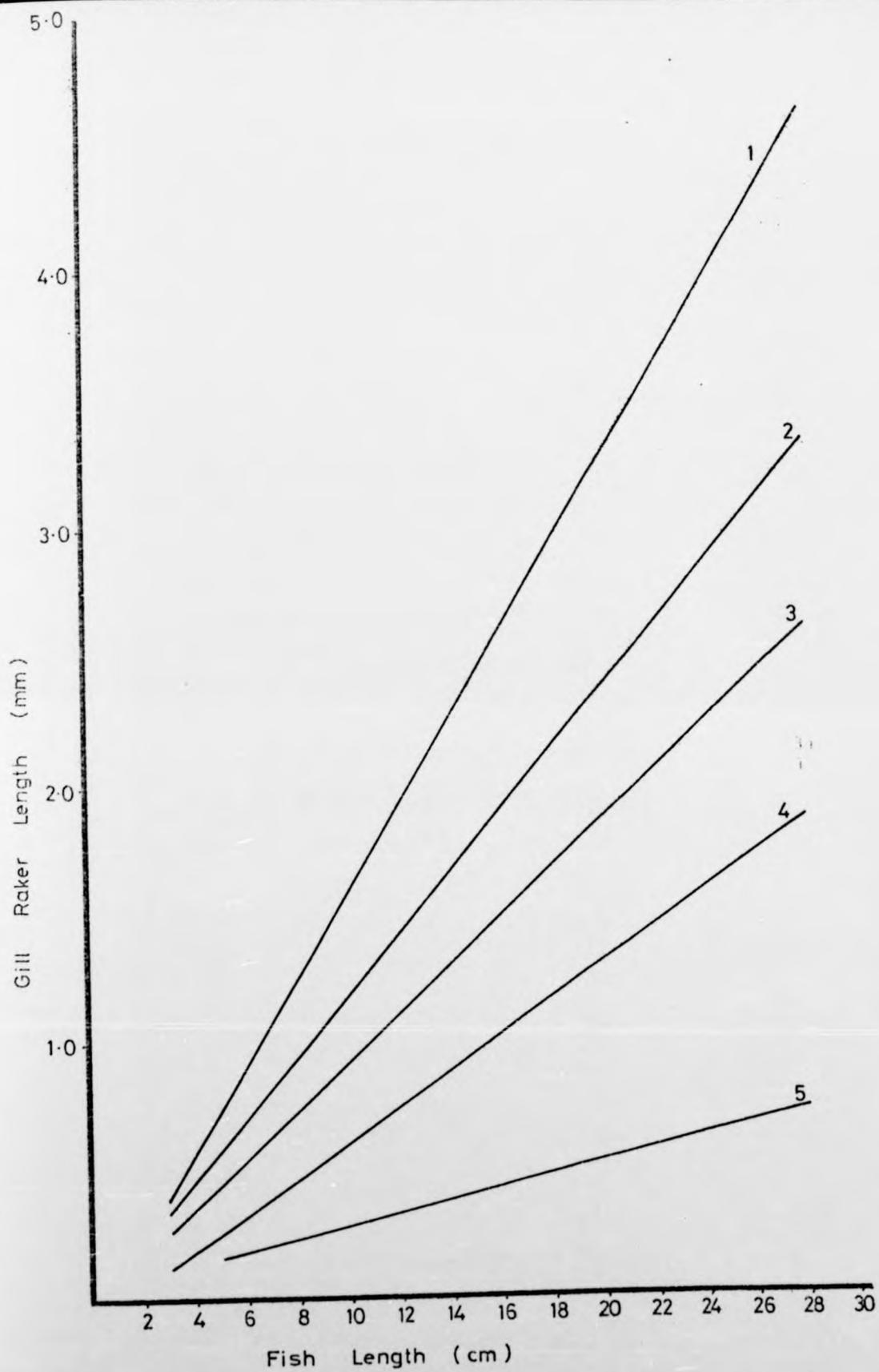
Fig. 4.   Gill raker spacing variation with fish length.

1   Mean (arches 1-5)

2   Range (arches 1-5)

.   Mean of 15 measurements (one fish)

3   Regression line, 1st arch only.

$r = 0.9755$; $P < 0.001$

Gill Raker Spacing (mm)

2·2

2·0

1·8

1·6

1·4

1·2

1·0

0·8

0·6

0·4

0·2
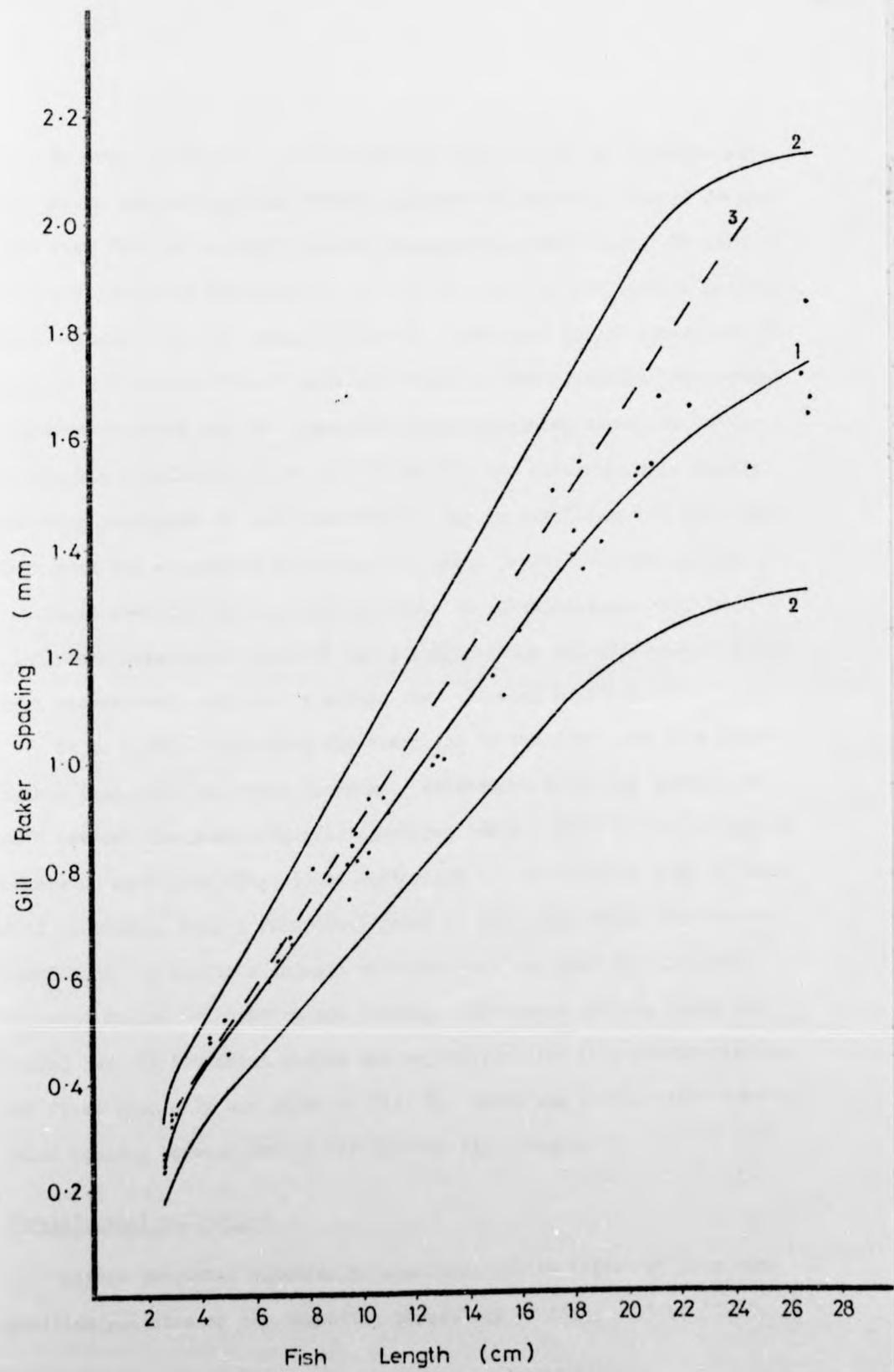
In order to quantify this screening with respect to particle size
the length of, and spacing between adjacent rakers was measured on the
same fish from which mouth breadth measurements were taken. In view of
the considerations mentioned above, and in order to standardise measure-
ments between fish and arches, only the three most dorsal rakers on the
ventral hemibranch of each arch were used for measurements. The oper-
culum was removed and the branchial arches stretched ventrally until
rakers lay parallel to each other (this did not alter spacing, merely
ensuring avoidance of raker convergence due to the V-shape of each arch).
Each arch was cleared of mucus and the raker length from the centre of
the basal swelling to tip, and the raker to raker distance half-way
along each raker were measured using a microscope and graticule. Arches
were successively removed to expose the following hemibranchs.

It is worth considering the branchial basket structure as a whole
rather than only the raker spacings. At maximum extension each raker
just covered the preceding gill aperture, hence a plot of mean length of
rakers on each arch (Fig. 3) is indicative of the relative size of each
gill aperture. From a functional point of view this would also corre-
spond with the relative amounts of water that can pass through each
aperture during respiration and feeding. The raker spacing (mean and
range) for all branchial arches and regression line from measurement on
the first arch only are shown in Fig. 4. There was little difference in
raker spacing between arches for any one fish length.

Physiological influences

Little published material is available on the effect of prey com-
position and size on the digestive physiology of fish. Elliot (1975, 3)

found that prey organisms on which brown trout showed a low feeding rate
and a long time interval between successive meals were also evacuated
from the gut at a slow rate compared to prey on which high feeding
rates and short inter-meal intervals were shown (Elliott, 1972, 2).
Gastric evacuation rate thus appears to depend on the type of prey
organism (Elliott, 1972, 2, and Thorpe, 1977), and also on the chemical
composition of the material fed (Windell et al, 1969 and Windell et al.
1972), the coarseness of the components comprising each pellet
(Tremieier and Deyoe, 1973 and Bergström pers. comm.), and the weight
of food taken in at one time (Windell et al, 1969 and Elliott, 1972, 2).
Prey resulting in high gastric turnover in the fish are likely to be
consumed at a higher rate and thus total food intake on particular prey
may closely depend on the rate of gastric evacuation.

Behavioural Influences

The effect of visual mechanics has already been extensively con-
sidered in Chapter 2. A direct consequence of visual acuity is the
reaction distance, i.e. the maximum distance at which the predator
responds to prey. The reaction distance in fish has been found to vary
with light intensity (Protasov, 1968) and turbidity (Moore and Moore,
1976). A direct relationship between prey size and reaction distance
has been found in mullet and horse mackerel (Protasov, 1968), cod
(Brawn, 1969), rainbow trout (Ware, 1972 & 1973), sunfish (Werner and
Hall, 1974) and flounder (Moore and Moore, 1976). Brawn (1969) found
that an abrupt decrease in reaction distance occurred with prey between
2 and 1 mm in length, presumably as a function of visual acuity.

100% Ingest

100% Rej

Fig. 5.   Prey size selectivity; capture, ingestion or rejection

behaviour.

100% Ingested 100 ─────────────────────────────── 0% Capture

80

60

40

20

100% Rejected 0 ─────────────────────────────── 100% Capture

0 109 0 155 0 218   0 435   0 875

Mean   Prey   Diameter   (cm)
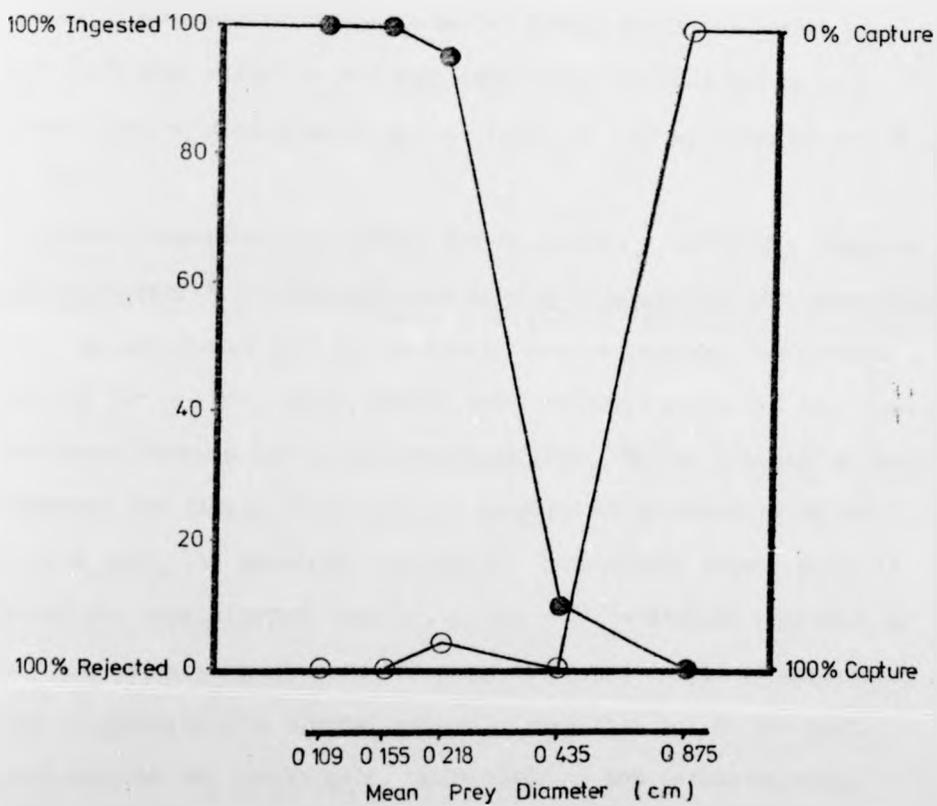
Protasov (1968) reports that above 7.5 cm (mullet) and 6.1 cm (mackerel)
prey length the reaction distance remained constant. A species-specific
upper size threshold may be due to behavioural selectivity mechanisms,
although the properties of light transmittance in water (Chapter 2)
affect contrast at a distance and response to this would be expected to
be species-specific. There is some evidence that reaction distance is
affected by movement of the prey: Boulet (1960) found that perch response
varied with prey velocity, and Ware (1973) reports that moving prey
improve reaction distances of rainbow trout by 0.22 m, irrespective of
prey size.

Simple behavioural preference for or against a particular item can
depend on a variety of factors based both on a population and individual
level. An individual predator is likely to have personal preferences
based on, for example, smell, taste, previous experience, and the size
relationship between itself and potential prey. On the population level
preferences are likely to be based on behavioural adaptations to the
available prey, its behaviour and habits. Thus simple measurements of
physical and physiological limitations may fail to explain rejection of
apparently suitable prey, this behaviour being the result of population
and/or species-specific specialisation on prey that has in the past
yielded maximum net energy gain, hence predator population success.

Fig. 5 is a diagrammatic representation of the results of capture
and subsequent behaviour taken from Table II, Chapter 2, indicating:

1) A threshold size between 0.0505 and 0.1015 of fish
   body length (0.435 and 0.875 cm mean diameter) above
   which prey were never captured, whereas below this

threshold all prey (bar one) within the reaction field
were captured.

ii) A second threshold prey size of between 0.0253 and
0.0505 of fish length (0.218 and 0.435 cm) below which
almost all captured prey were ingested, above which
almost all were rejected.

Superimposition of this pattern of selective behaviour on plots of
mouth breadth and gill raker spacing (Fig. 6) clearly shows that pro-
nounced prey size selection occurs within the potentially available
range of prey defined by these parameters.

A final consideration must be given to the motivational state of
the fish. Excluding effects such as previous experience the major
influences at any one time on prey choice, and indeed whether to feed or
not, are hunger and rhythmic diel feeding activity. The existence of
diel feeding rhythms in salmonids, and their periodicity, has already
been discussed in Chapter 1, and it remains only to state the obvious
conclusion that reaction and preference behaviour will depend on the
part of the feeding cycle under consideration. However it appears
likely that feeding rhythms in these fish are closely related to diel
cycles of prey abundance (p. 31), and it may be that inherent diel
feeding rhythms are of little consequence.

Hunger represents a strong motivational control of feeding activity
and intensity. The rate of attack on prey by rainbow trout (Ware, 1972)
and sunfish (Werner, 1974) has been shown to decrease exponentially with
time. Ishiwata (1968) has demonstrated that the amount of food required
to satiate rainbow trout increases to a maximum when stomach contents

approach zero. Ivlev (1961) found that prey selectivity depended on the amount of food already consumed.

CONCLUDING COMMENTS

Fig. 6 summarises mouth breadth and raker spacing change with fish length. If mouth breadth and raker spacing directly control the maximum and minimum sizes of potential prey then it can clearly be seen that the range of available prey increases with fish length increase. However if the available prey size range in each case is expressed in terms of the respective fish body length the result is 0.06 body lengths throughout the range of fish sizes shown. Thus it can be concluded that the potential available prey range remains constant relative to the length of the fish. From Fig. 6 it can also be seen that selection by fish of length 8.6 cm took place for prey sizes within the lower third of this range and against prey sizes in the upper third. Prey larger than mouth gape were outside of the range captured.

Fig. 6. Relationship between mouth breadth, raker spacing and
percent of captured prey ingested (Table II, Chapter 2).

IMB – Internal mouth breadth

GRS – Gill raker spacing

I – Ingested

C – Captured

and

er 2).
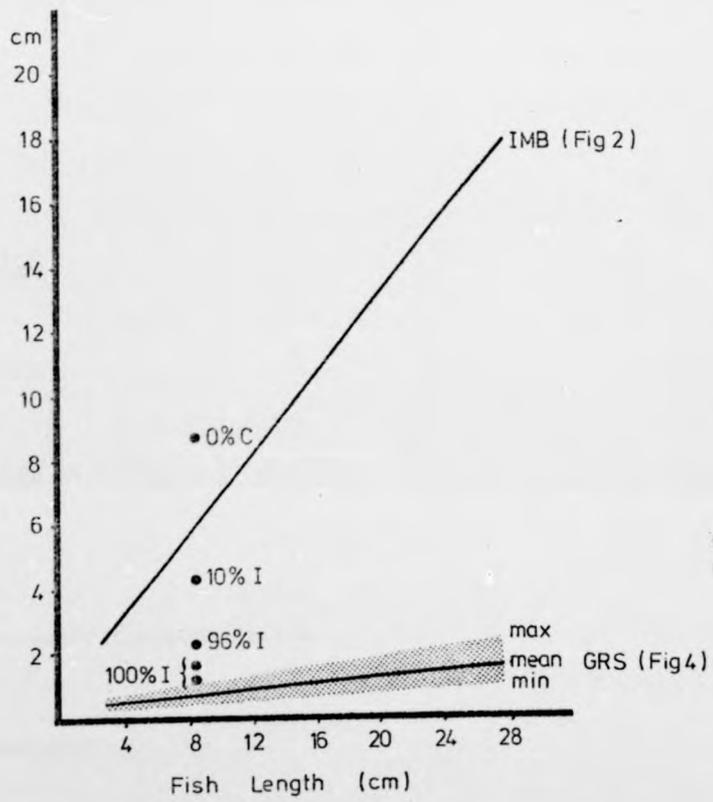
Chapter 4

GROWTH AND PREY SIZE

INTRODUCTION

EXPERIMENTAL MATERIAL

METHODS:

Experimental tanks

Diet

Feed dispensers

Illumination and water characteristics

Cover rings

Experimental procedure

RESULTS

DISCUSSION

CONCLUSIONS

INTRODUCTION

Certain teleost fish (including salmonids) show a high degree of prey selection which is based on body size, the evidence for which is extensively reviewed elsewhere (Chapter 3). Prey selectivity implies a mechanism for optimising foraging efficiency, and thus in the case of immature fish that are not developing gonadal tissues, maximising potential somatic growth. The importance of the relationship between prey size and predator size in fish, from the point of view of the efficiency of energy gathering and utilisation, has been demonstrated in several recent excercises in mathematical modelling (Paloheimo and Dickie 1965 & 1966, Kerr, 1971, 1) and speculations on the importance of increasing prey size with increase in fish size have been made by Brett (1970) and Elliot (1975) amongst others.

Experimental evidence on the effect of prey size on fish growth has been, however, inconclusive. Le Brasseur (1969) found that the growth of chum salmon juveniles (Onchorhynchus keta) was not significantly affected by the size of available prey, but his prey size categories were exclusively composed of different species or taxa and prey was continually available at abnormally high densities (thus potentially masking differences in prey size related to foraging efficiency, Le Brasseur loc. cit.). Nakamura and Kasahara (1956) found improved growth in populations of carp fed on mosquito larvae and cladocerans retained by a 400 micron mesh when compared with those fed only on cladocerans smaller than 400 microns body size. Grassle (1957) found that the smallest of 3 sizes of pellet gave the fastest weight recovery on transference of rainbow and brook trout from natural to artificial diets, and Prather (1958) reports that fathead minnows   showed highest survival rate, weight gain, and conversion efficiency on the largest of three particle sizes of artificial feed offered, although the results were not statistically significant.

The increasing use of pelleted artificial diets in the aquaculture industry since the late 1950's has resulted in the development of empirical

rules relating the size of pellet to be fed to fish of a particular size-class (Hastings and Dickie 1972). These were initially based on subjective evaluation (e.g. Phillips 1956) but have recently been refined by studies of acceptance-rejection behaviour (Fowler and Burrows 1971). Within the commercial feed manufacturing sphere the production, and hence availability, of feeds of particular particle size has been governed all to often by the economics of manufacturing and particle size separation processes (Robinson 1971, Stivers 1971, and Cooper Nutrition Products Ltd., G.B., pers. comm.) and recommendations have been based on experience rather than experiment (Trouvit Ltd, G.B., Silver Cup, E. Langvad Jensen, Denmark, Skretting AB, Sweden; all pers. comm.).

The use of live prey to study the growth response of fish to prey of different size categories is severely handicapped by the insurmountable difficulty of obtaining a wide size range of otherwise identical organisms (Cf. Nakamura and Kasahara 1956, Le Brasseur 1969). This is fundamental to investigation of growth response as the potentially useful energy per unit weight of prey material and the digestive response of the predator must be comparable between prey categories. Elliot (1972 and 1976) has clearly shown that both these factors vary with the type of prey organism.

For the present study it was therefore decided to use artificial pelleted feeds, whose composition and particle size could be rigidly controlled and which presented no problems of availability. This chapter reports a series of short-duration experiments made to determine the growth response of juvenile Atlantic salmon to diets composed of different particle sizes.

EXPERIMENTAL MATERIAL

Atlantic salmon juveniles of known origin and environmental history
(obtained as described in Chapter 2, p 46) were maintained at ambient
water temperatures in 2 m diameter circular rearing tanks (described by
Minaur 1973, and Billard and Petit 1973) at the Department of Agriculture
and Fisheries for Scotland, Freshwater Fisheries Laboratory, Faskally,
Perthshire, Scotland. Rearing tanks were essentially larger versions of
the experimental tanks described in the following section, with the
exception that solenoid-operated drawer-type feed dispensers (Minaur 1971)
were used. Feeding period was time-switch controlled, commenced at dawn
and terminated at dusk. Stock fish were fed on a diet of Ewos salmon
feed (Astro-Ewos AB, Sweden) in accordance with the manufacturers
recommendations. Although feed particle size was increased as fish grew
(Table 1) a wide range of particle size was made available to the fish at
any one time (Fig 1) and size categories (Ewos 1, 2, 3 and 4) were
overlapped during the protracted periods of changeover from one size
category to the next (i.e. for approximately 50% of the time). Fish
were initially stocked at 2000 alevins per tank, this density was progress-
ively reduced over two years until at the end of the summer of their second
year the stocking density was approximately 500 fish per tank.

FIG 1   Stock Fish Diet Particle Size Composition

Relative frequency by weight

.5
.4
.3
.2
.1
0

.5
.4
.3
.2
.1
0

.5
.4
.3
.2
.1
0

.5
.4
.3
.2
.1
0

.18

Relative frequency by weight

EWOS 4

EWOS 3

EWOS 2

EWOS 1

Feed diameter (mm)

.18 .25 .36 .50 .71 1.00 1.40 2.00 2.80 4.00 5.60 8.00
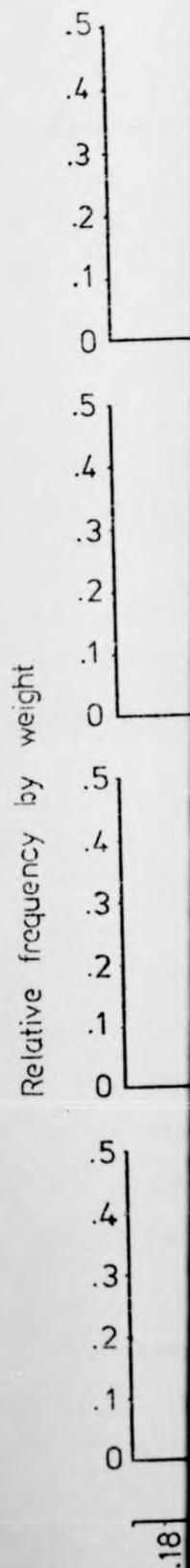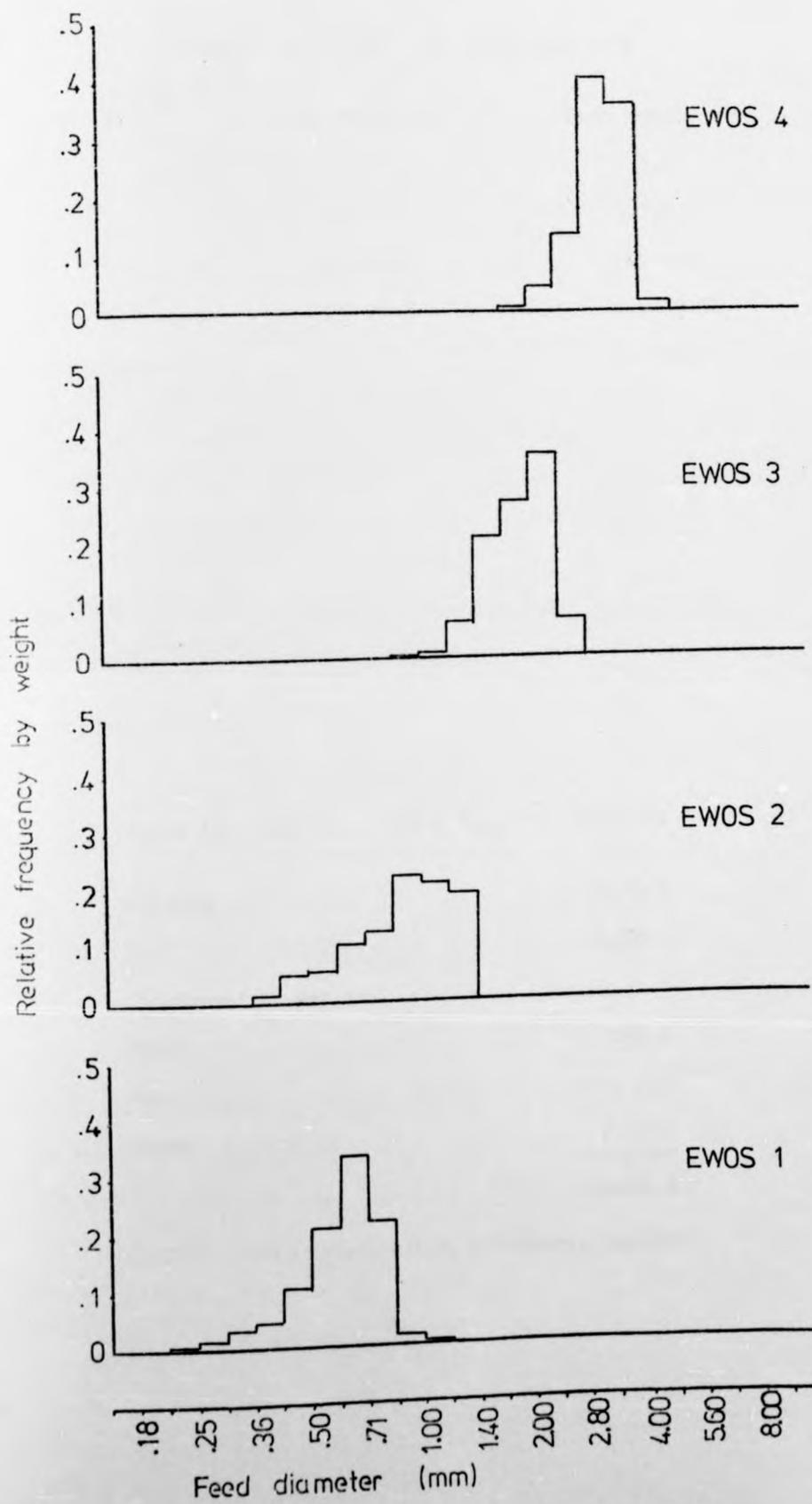
Table I. Ewos food size recommendations

Food size	Fish weight(gm)	Fish length(cm)
1	0.4	3.5
2	0.4-3.0	3.5-7.5
3	3.0-15.0	7.5-11.0
4	15.0-40.0	11.0-16.0
5	40.0-75.0	16.0-20.0

Table II. Analysis: Silver Cup, Superspeed II

Protein	47.69 %
Fat	8.65 %
Nitrogen-free material	20.81 %
Fibre	2.40 %
Ash	11.45 %
Water	9.00 %
	100.00 %

SCURCE:- Steins Laboratorium, København, Denmark

METHODS

Several tanks with feed dispensers were used. The basic components of each are described in the following sections, with comments on the entire experimental apparatus where appropriate.

1. Experimental tanks (Fig 2)

Tanks were made of glass-fibre reinforced polyester resin, smooth on the inside with self coloured black base (1) and white sides (2) and a curved transparent sheet-acrylic window (3) inset along one-third of the circumference to enable observations to be made without disturbing fish. A valve controlled the volume of water entering at the central input (4) the flow was then deflected by the base and formed a current cell as indicated. Water was voided from the tank by the circumferential drain (5) and two standpipes (6) the height of which could be adjusted to maintain the required water depth (7).

Food particles entered the tank via the central water input pipe and were carried radially by the water current above the tank base towards the circumferential drain. Perforated drain covers retained fish within the tank but allowed food particles that were not captured by fish to be immediately voided from the tank. By using different drain covers the aperture size could be chosen to be larger than food particle size, thus obviating the possibility of food retention and break-up within the tank and consequent alteration of particle size.

A flat aluminium ring (10) suspended just above the tank base, provided cover for fish within the tank (see also section 5, p 116). A ½ inch (1.27 cm) mesh nylon net covered the tank to prevent fish leaping out.

2. Diet

Silver Cup salmon feed Super Speed II (Silver Cup, E Langvad Jensen, Denmark) was used as the experimental diet. All food used was of the same formulation (Table II) and particle diameters from 0.018 to 1.32 cm were obtained by grinding then sieving into discrete size classes (Table III)

FIG. 2. Experimental Tanks.

Top. side view

Bottom. plan view

Legend: 1   Tank base

2   Tank side

3   Acrylic window

4   Central water inlet

5   Circumferential drain

6   Standpipe

7   Water surface

8   Current cell

9   Mains water input

10   Cover ring

11   Food input
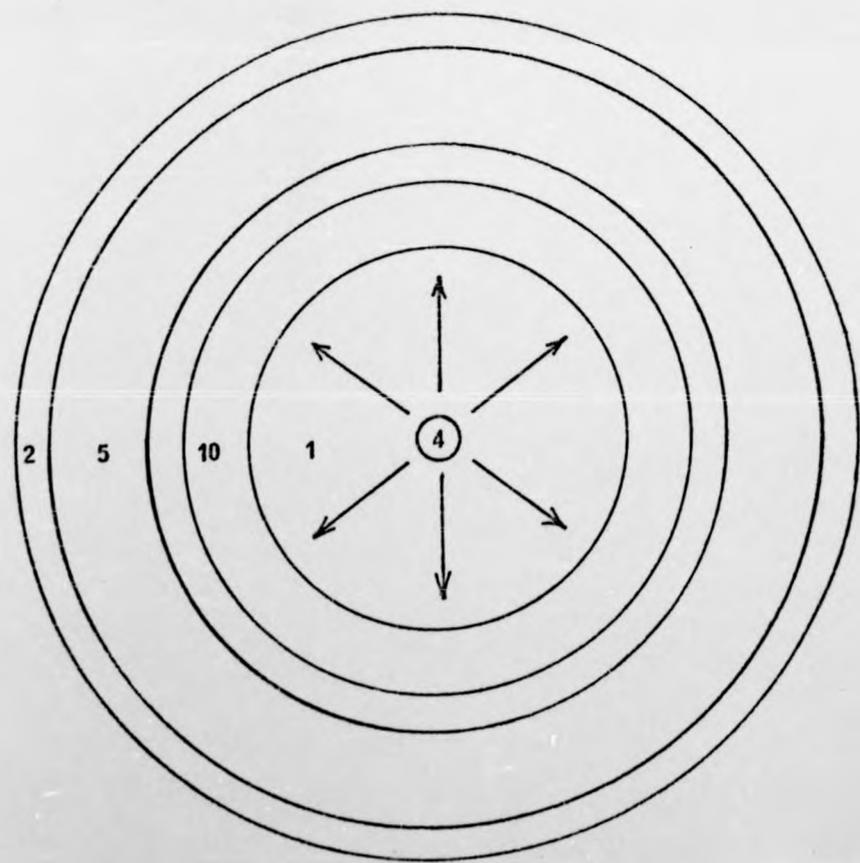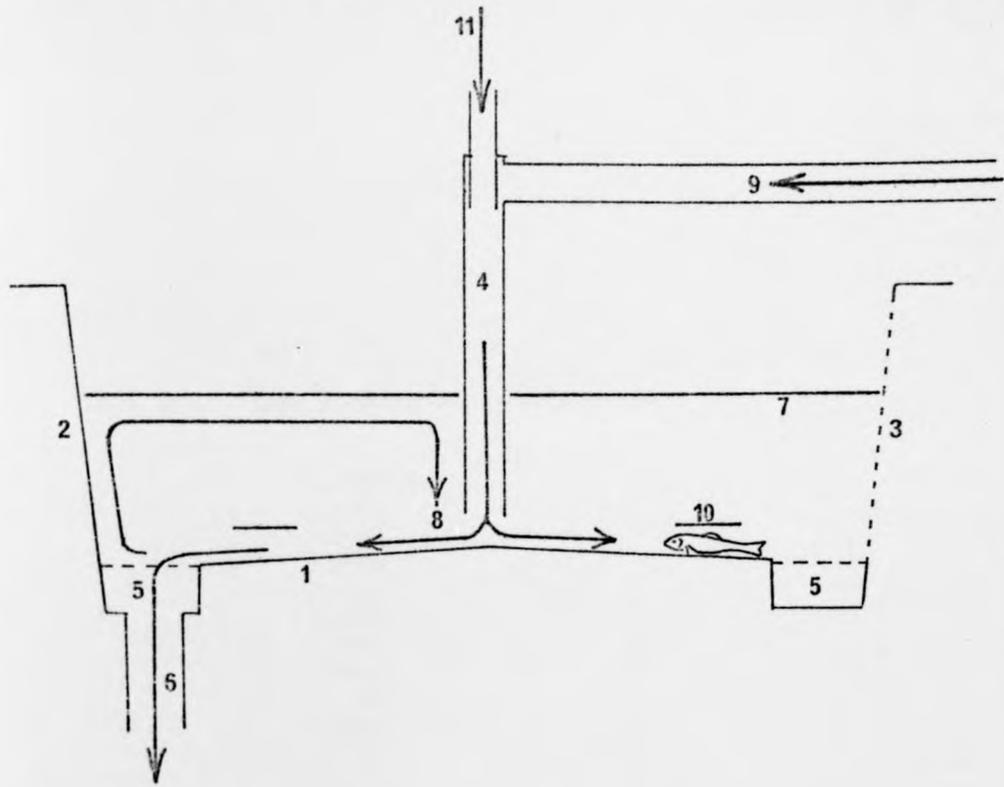
Table IV. Silver Cup feeding regime. Percent body weight per fish per day.
(Manufacturers recommendations)

Temperature degrees C	Mean weight of fish (gm)							
	-0.18	0.18-1.49	1.49-5.00	5.00-12.5	12.5-25.0	25.0-40.0	40.0-62.5	62.5-100.0
2	2.7	2.2	1.7	1.3	1.0	0.8	0.7	0.6
3	2.8	2.3	1.8	1.4	1.1	0.9	0.7	0.6
4	3.0	2.5	2.2	1.7	1.3	0.9	0.8	0.7
5	3.3	2.8	2.2	1.8	1.4	1.1	0.9	0.8
6	3.6	3.0	2.5	1.9	1.4	1.2	1.0	0.9
7	4.0	3.3	2.7	2.1	1.6	1.3	1.1	1.0
8	4.1	3.4	2.8	2.2	1.7	1.4	1.2	1.0
9	4.5	3.8	3.0	2.4	1.8	1.5	1.3	1.1
10	5.2	4.3	3.4	2.7	2.0	1.7	1.4	1.2
11	5.5	4.5	3.6	2.8	2.1	1.7	1.5	1.3
12	5.8	4.9	3.9	3.0	2.3	1.9	1.6	1.4
13	6.1	5.1	4.2	3.2	2.4	2.0	1.7	1.4
14	6.7	5.5	4.5	3.5	2.6	2.1	1.8	1.5
15	7.3	6.0	5.0	3.7	2.8	2.3	1.9	1.7
16	7.8	6.5	5.3	4.1	3.1	2.5	2.0	1.8
17	8.4	7.0	5.7	4.5	3.4	2.7	2.1	1.9
18	8.7	7.2	5.9	4.7	3.5	2.8	2.2	1.9
19	9.3	7.8	6.3	5.1	3.8	3.0	2.3	2.0
20	9.9	9.4	6.9	5.5	4.0	3.2	2.5	2.1

Table V. Weight to volume conversion factor data

Particle diameter	Weight per 250 cm³ (mean of three measurements)	Volume per gm
(cm)	(gm)	(cm³)
0.170-0.200	137.0	1.825
0.200-0.236	138.5	1.805
0.236-0.280	137.0	1.825
0.280-0.335	145.3	1.721
0.475-0.560	143.2	1.746
0.670-0.800	135.4	1.846
1.12 -1.32	142.0	1.761

Table VI. Aluminium Cover Ring sizes

Fish lengths accomodated	Ring width	Inner diameter of Ring
(cm)	(cm)	(cm)
-3.5	2.0	7.2
3.6-4.5	2.7	9.6
4.6-5.5	3.3	12.0
5.6-6.5	4.0	14.4
6.6-7.5	4.7	16.8
7.6-9.0	5.3	19.2
9.1-12.0	6.7	24.0
12.1-16.0	9.3	33.6
16.0-	12.0	43.6

using a set of close-tolerance test sieves (Endecotts Ltd, London, G.B.). The manufacturers feeding recommendations were observed as to feed weight, fish size and water temperature interrelations (Table IV). The feed dispensers delivered food on the basis of volume and not weight hence a conversion factor was determined as follows:

A quantity of feed of each of seven particle size ranges was settled in a measuring cylinder by administering several sharp taps until packing was no further improved. The weight of 0.25 l was determined and the volume per gram calculated (Table V). The mean conversion factor was found to be 1.790 $cm^3 gm^{-1}$.

Hence by calculation from Table IV the volume of food required **per** fish per day could be determined. This mean conversion factor was used throughout the range of particle sizes used.

3. Feed dispensers

Conventional feed dispensers operate on the principle that a discrete volume of food particles is dispensed at intervals of time during the feeding period. Since the purpose of the experimental design was to maximise feeding opportunity on a limited quantity of feed and also minimise food particle residence time in the tank it is clear that a large number of food particles entering the tank at one time would have been unsatisfactory. Furthermore accurate control of the amount of food input per day was also necessary. Consequently a dispenser was designed which would only release small quantities of food particles during the feeding period, and the output of which could be calibrated and thus controlled.

Essentially the feed dispenser (Fig 3) consisted of a PVC cylinder (1) through which a close-fitting cast polyester piston (2) was pulled at a constant rate. The cylinder was filled with particulate feed of the required particle size. The pulley (3) rotated by the geared electric motor (1 rev per 24 hours, maximum load 10 cm Kg) (4, Crouzet Ltd, G.B.). The whole assembly was mounted on a strong acrylic frame, both the cylinder

FIG. 3. Feed Dispenser design.

Top. end view

Bottom. side view

Legend:
1 PVC cylinder, internal diameter D

2 Piston, external diameter D

3 Pulley wheel

4 Geared electric motor

5 Pulley pins (ϵ), adjustable to give radius R

6 Steel monofilament wire

7 Secondary pulley

8 Water input

9 Funnel, top diameter 25 cm

10 Water + feed outlet to experimental tank
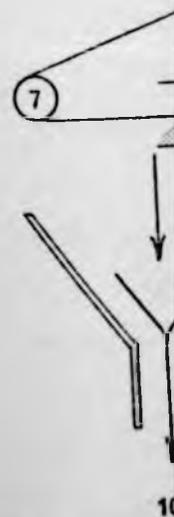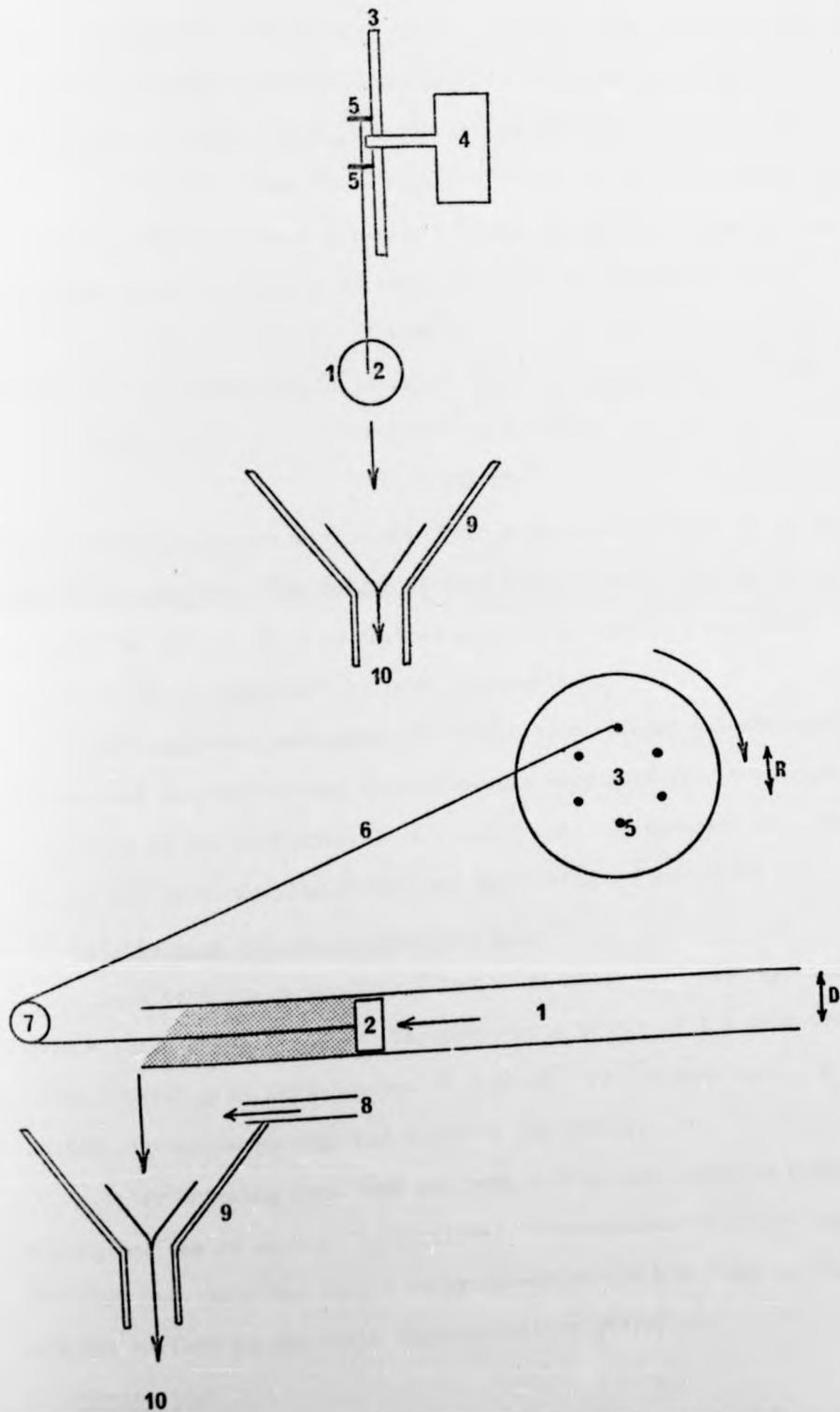
and piston assembly and the pulley wheel being removable.

The cylinder and piston assembly was replaceable enabling different diameter assemblies to be used (0.820, 1.775, 2.890, 4.175, 5.215 and 7.690 cm internal diameter). Similarly the effective pulley radius could be altered by repositioning of the six pulley pins (from 0.5 to 3.5 cm, in 0.5 cm steps). Thus for a required volume of food (V) to be delivered over a feeding period of duration T hours the pulley radius (R) and cylinder diameter (radius r) required could be calculated from:

$$V = \pi r^2 L$$

where L, the piston displacement per daily feeding period = $\dfrac{6R. \ T}{24}$

Thus $\quad\quad\quad\quad\quad\quad\quad V = (\pi r^2)(6R. \ T/24)$

i.e. $\quad\quad\quad\quad\quad\quad\quad V = 0.772 \ RTr^2$

Feed dispensers were tested over a period of 5 days at 16 hours of operation per day. The weight of feed dispensed per day was found to deviate by -2 to -5 from that expected from calculations, which represents a high level of agreement between dispensers.

The cylinders were normally re-filled at 10 day intervals, although longer and shorter between fill intervals were sometimes necessary depending on the combinations of r and T used. Dispensers were switched on and off (i.e. feeding period per day) using a time-switch.

4. Illumination and water characteristics

Each tank was separately illuminated by one 200 Watt incandescent bulb mounted directly above its centre at a height of 1 m from the tank base, providing an illumination of 2.32 WM^{-2} at the tank base. A time-switch controlled photoperiod duration and timing.

Water entering each tank was pumped from Loch Faskally through PVC piping and was at ambient temperature. Temperatures of outlet water were recorded once each day in the early afternoon and are shown in Fig 4, as are the periods during which experiments were conducted.

5. Cover rings

Within the radial flow experimental tank current and food distribution

FIG 4. Water temperature regime during experimental runs
(recorded daily at 16 00 hrs)

22
20

runs
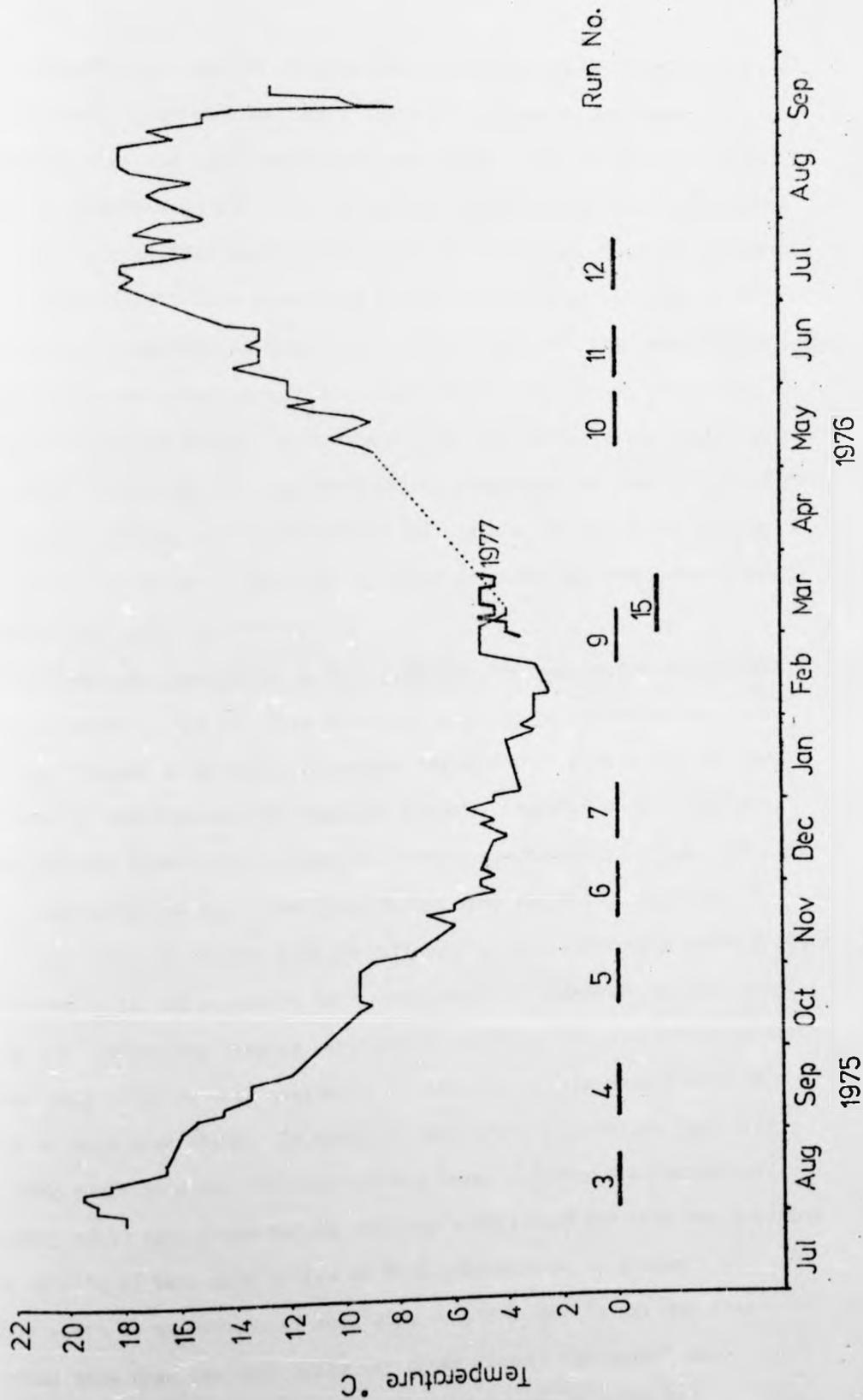
were predominantly equally distributed in all directions from the central water input. Feeding opportunity for each fish would therefore be maximised when the fish were distributed equally around the water input pipe, facing towards it. Atlantic salmon juveniles **orientate** directly into the current (Chapter 1) and, within the environment of the experimental tanks maintained bottom-associated positions when possible. However preliminary experiments showed that socially dominant fish monopolised large areas of the tank bottom with the result that up to 22 out of 24 fish were found to hold mid-water positions and thus being effectively denied access to food. This behaviour was particularly pronounced in some groups of fish during the summer, but absent during the winter. It was found that by the provision of cover this type of overt dominant and submissive fish distribution could be avoided.

Cover was provided by a flat aluminium ring suspended within each tank as shown in Fig 2. This cover was found to be effective only when the gap between cover ring and bottom was such that fish could fit into it only if their dorsal fin remained folded. Provided these conditions were met all fish within a tank held bottom-associated positions and almost all remained below the cover ring, facing into the bottom current.

In order to provide fish in different size classes with equal feeding opportunity it was necessary to relate cover ring diameter to fish size. This was achieved by keeping constant the ratio of the proportion of the cover ring circumference available to each fish to the mean length of fish in each size class. In addition this prevented smaller fish from holding position above the drain cover, hence ensuring that potential feeding could take place before food was voided from the tank and avoiding the effects of tank-side eddies on fish orientation. Adjustment of cover width to two-thirds of mean fish length helped to prevent fish forming more than one rank under the cover rings. The cover ring dimensions used for each fish size range are shown in Table VI.

The rate of water input was adjusted such that when ejected from

the input pipe feed particles of the largest size used in any one
experiment were carried and deposited below the cover ring inner edge.
This rate of inflow was found to be satisfactory as fish were prevented
from coming closer to the tank centre than the inner edge of the cover
ring but were still able to hold position below it. After deposition
food particles were swept into the circumferential drain within 1-2
minutes.

6. Experimental procedure

Six tanks, in two rows of three facing each other, were used throughout, and each tank was fitted with its own feed dispenser and light source as described. The only source of illumination were the six lights which were synchronously switched on and off. The photoperiod remained constant throughout any one experiment at that naturally occuring half-way through the period of each experiment (Table VII).

The mean size of stock fish in one rearing tank was determined by sub-sampling and 180 fish of a length close to this mean removed from the same tank. Thirty fish were placed in each experimental tank under the selected photoperiod and starved for 48 hours prior to measuring and weighing. Brett and Higgs (1970) have shown that the rate of gastric evacuation in sockeye salmon fed on Abernathy pellets was dependant on water temperatures: after 48 hours stomachs were at least 99% empty at temperatures of 7.5 degrees C and above, 90% empty at 4.5 degrees C, and 75% empty at 3.0 degrees C. Similarly Elliott (1972) found that brown trout stomachs were at least 90% empty after 48 hours at 5 degrees C and above, independant of the type or amount of live prey consumed. The period of 48 hours starvation thus represents a period at the end of which it is likely that all stomachs would have been at least 90% empty, thus almost eliminating between-fish error on weighing due to possible variations in previous meal size and timing, except in the case of experimental run number 9 which was commenced at a temperature of 3 degrees C.

Fish were anaesthetised in MS222 (Sandoz) and then measured (snout to fork) to the nearest 0.1 cm, surface dried on absorbent paper, and individually weighed to 0.01 gm. Twenty four fish were assigned to each tank such that maximum deviation did not exceed $\pm$ 7.5% of mean length. Maximum mouth breadth was determined on a sub-sample of 8-10 fish.

By determination of the mean fish weight and measurement of water temperature, the food weight requirements were obtained from Table IV and converted to volume enabling feed dispenser parameters to be calculated.

All feed dispensers operated synchronously and the feeding period was
always set to commence at least half an hour after the lights had come
on and terminate before the lights were switched off at the end of the
"day". The maximum feed particle size chosen was that obtained from the
pair of sieves immediately larger than those of aperture size within which
the mouth breadth measurement fell. The full range of feed sizes used
was obtained by reducing particle diameter by half in each case until six
size ranges were obtained. For example:

Maximum mouth breadth - 0.51 cm

		Code	Particle diameter range (cm)
Maximum feed size	(100%)	F	0.56 - 0.67
	50%	E	0.28 - 0.34
	25%	D	0.14 - 0.17
	12.5%	C	0.071 - 0.085
	6.25%	B	0.036 - 0.043
	3.125%	A	0.018 - 0.021

Feed sizes were assigned one to each tank on a random basis.
Feed dispensers were put into operation and cover rings installed in each
tank on the day following weighing and measuring. The total duration of
the feeding part of each experiment was 20 days. At the end of this period
the feed dispensers were switched off and fish starved for a further 48
hours prior to final weighing and measuring in the manner already described.

In total 9 complete experiments were conducted, alternating 0+ and
1+ fish, during the latter part of 1975 and first half of 1976, with
one experiment during early 1977. A summary of experiments is given in
Table VII.

Although a wide range of particle sizes was given to stock fish
there was still the possibility that particular sizes of fish might have
become pre-conditioned to feed on particular feed sizes. In order to
examine this possibility the fish used in experimental run 12 were fed
only on Ewos size 1 (Fig 1) prior to the experiment, although they should

Table VIIa Details of experimental feeding regimes and photoperiod

See also Fig. 4, Tables III and IV.

Experiment Run Number	Mean initial fish length (cm)	Mean feed particle diameters						Photoperiod duration (hrs)
		A	B	C	D	E	F	
3	6.7	0.019	0.039	0.078	0.155	0.308	0.617	15
4	17.7	0.055	0.109	0.218	0.438	0.875	1.220*	14.5
5	9.2	0.028	0.055	0.109	0.218	0.438	0.875	10
6	20.3	0.055	0.109	0.218	0.438	0.875	1.220*	7.5
7	9.8	0.028	0.055	0.109	0.218	0.438	0.875	7
9	10.5	0.033	0.066	0.129	0.258	0.517	1.035	10.5
10	2.8	-	0.017	0.032	0.066	0.129	0.258	16.5
11	8.6	0.023	0.046	0.093	0.185	0.367	0.735	17.5
12	4.2	0.017	0.028	0.055	0.109	0.218	0.438	17
15	13.4	0.039	0.078	0.155	0.308	0.615	1.220	11.25

NB Runs 1,2,8,13 & 14 were either preliminary experiments or part of unrelated experimental work. A-F designate treatments, not experimental tanks which were assigned randomly (Table VIIb)

* Size F should have been 1.750 cm diameter but due to unavailibility of this feed size the largest available (1.220 cm) was substituted.

Table VIIb. Details of treatment assignation by tank number.

Experiment Run Number	Treatment A	B	C	D	E	F
3	4	1	5	6	3	2
4	2	4	6	5	3	1
5	6	3	2	5	4	1
6	2	5	6	1	4	3
7	2	5	6	3	1	4
9	6	1	5	4	3	2
10	1	4	6	3	2	5
11	4	6	3	5	2	1
12	2	3	6	1	5	4
15	6	1	5	4	3	2

have been fed size 2 on attaining a length of 3.5 cm (Table I).
Inspection of the results shows that maximum growth was shown on feed
particles 0.100 to 0.118 cm in diameter, although the largest size present
in a significant amount in Ewos size 1 feed was 0.071 to 0.085 cm.

Four separate family groups, each the progeny of one parental pair
were studied in order to complete almost all the experimental series in
the course of one year. The break-down by family, year class, and source
for each experiment is shown in Table VIII. The situation was complicated
by the development of a bimodal size-frequency distribution in the
population of each rearing tank amongst fish hatched in 1975 and 1976 which
became apparent in the autumn of their first year (Thorpe 1977, 2). In
all cases the larger mode attained a length of 9 - 10 cm by the winter
of their first year and underwent changes associated with smoltification.
These fish were therefore not used for further experiments after the
following March and the growth responses of fish in their second year
(1+) were studied only on fish from populations showing a unimodal
distribution or from the original lower mode. In March 1977 smolts from
1975 hatched smaller mode fish were studied (run 15). Hence the growth
responses of fish undergoing final changes associated with smoltification
from both the smaller (run 9) and larger (run 15) length modes were
studied.

The experimental run using first feeding alevins (run 10) was
commenced when the dry weight ratio embryo:embryo + yolk, determined by
sub-sampling the stock, had reached a mean value of 0.80. One hundred
fish were stocked in each experimental tank from which a sub-sample of
24 was weighed and measured at thestart and end of the run. As initial
lengths of fish were very uniform no adjustment of the initial size
distribution was necessary.

Table VIII. Sources of experimental fish, arranged in order of age (youngest at top)

Year of hatching	1976(I)	1975(I)		1974(II)	Age of fish when used in experiment	
Family group	a	b	c	d		
Experimental Run	10 12	3			0+	Experimental fish represented mean length of population
		5* 7 9(III)	11*			Experimental fish represented mean length of larger mode of population
						..mean length of smaller mode
				4 6	1+	Experimental fish represented mean length of population
			15(IV)			..mean length of smaller mode

Notes: (I)   Populations developed bimodal size-frequency distribution
        (II)   Populations remained unimodal
        (III) Larger mode smolts (as 0+)
        (IV)   Smaller mode smolts (as 1+)

  *   Fish of comparable length

RESULTS

Growth in weight and length. Initial, final and change in weight of fish on diets of each particle size for each experimental run are presented in Table IX. Standard deviations for means of initial and final fish weights are also given as is the temperature regime experienced by fish during the experimental runs. The results are set out in order of fish age, as shown in Table VIII.

Statistical treatment. Deviations from zero change in weight were examined using the Students t-test. Since standard deviations of initial and final weights were similar the following formula was used:

$$t = \frac{\overline{X}_2 - \overline{X}_1}{\sqrt{\dfrac{N_1 S_1^2 + N_2 S_2^2}{N_1 + N_2 - 2}} \sqrt{\dfrac{N_1 + N_2}{N_1 N_2}}}$$

where: $\overline{X}_1$ & $\overline{X}_2$ = means of initial and final weights

N_1 & N_2 = number of fish at start and end of experiment

S_1 & S_2 = standard deviations of initial and final weights

(from . Blalock 1972)

The results of these tests are shown in Table X.

Graphical representation. The results are presented in graphical form in Figs. 5 to 14, which show:

1) Mean change in weight as percentage of mean initial weight, 2) mean change in length as percentage of mean initial length,

Plotted against the ratio mean feed diameter: mean fish length (P.F.R.) which is a measure of relative feed size. The level of significance of each weight change is also indicated on each fig.

Summary. In June and July (mean temperatures 13.0 - 17.2 degrees C) the optimum P.F.R. was 0.022 - 0.026 but a significantly good growth rate was also shown at 0.044 - 0.052. In August (18.5 degrees C) optimum P.F.R. was 0.022 - 0.026. During September and October (14.1

and 9.3 degrees C) optimum F.F.R. remained the same but only slightly
poorer growth rates were shown at 0.012 - 0.013. During the winter
(November and December, 5.5 and 4.4 degrees C) this trend continued
with maximum growth in weight being shown at a F.F.R. of 0.011 only.
Fish smoltifying during their first or second year (as 0+ and 1+
smolts, February and March) as water temperatures were commencing to
rise (4.5 degrees C) showed comparable maximum growth rates at
F.F.R.s of 0.012 and 0.024.

Table IX. Results of growth experiments on prey of different particle size.
(ranked in order of fish age)

Run	Mean temp. deg.C	Mean feed diameter cm	Code	Mean initial weight gm	SD	Mean final weight gm	SD	Weight change gm	Mean initial length cm	SD	Mean final length cm	SD	Length change cm	Mortality No./24
10	9.9(i)	–	A	0.168	0.011	0.178	0.005	0.010	2.85	0.051	2.92	0.059	0.071	–
		0.017	B	0.172	0.010	0.185	0.003	0.013	2.85	0.051	2.93	0.048	0.088	–
		0.033	C	0.171	0.011	0.206	0.006	0.035	2.85	0.051	2.98	0.082	0.138	–
		0.066	D	0.171	0.009	0.207	0.005	0.036	2.85	0.051	3.00	0.069	0.150	–
		0.129	E	0.169	0.012	0.202	0.007	0.034	2.85	0.051	2.97	0.104	0.121	–
		0.258	F	0.170	0.009	0.207	0.006	0.038	2.85	0.051	2.99	0.074	0.133	–
12	17.2(s)	0.017	A	0.689	0.072	0.704	0.064	0.015	4.15	0.147	4.22	0.382	0.670	3
		0.028	B	0.635	0.071	0.693	0.065	0.058	4.10	0.146	4.20	0.410	0.100	0
		0.055	C	0.680	0.086	0.803	0.072	0.123	4.14	0.162	4.35	0.463	0.209	1
		0.109	D	0.657	0.083	1.192	0.079	0.535	4.14	0.164	4.82	0.412	0.679	0
		0.218	E	0.696	0.078	1.140	0.070	0.444	4.20	0.158	4.76	0.378	0.559	7
		0.438	F	0.684	0.074	0.914	0.056	0.231	4.16	0.150	4.46	0.294	0.300	8
3	18.5(d)	0.019	A	3.322	0.442	2.851	0.369	-0.471	6.69	0.254	6.63	0.254	-0.063	0
		0.039	B	3.333	0.462	2.916	0.496	-0.417	6.73	0.291	6.64	0.313	-0.089	5
		0.078	C	3.330	0.439	3.075	0.596	-0.255	6.72	0.253	6.73	0.322	0.008	0
		0.155	D	3.249	0.412	4.448	0.525	1.199	6.67	0.272	7.30	0.249	0.639	1
		0.308	E	3.325	0.386	3.122	0.524	-0.203	6.72	0.237	6.77	0.301	0.048	1
		0.615	F	3.283	0.392	3.117	0.494	-0.166	6.65	0.257	6.74	0.312	0.087	0
5	9.3(d)	0.028	A	8.825	1.141	8.067	1.046	-0.758	9.25	0.361	9.15	0.558	-0.104	0
		0.055	B	8.895	0.982	8.118	0.890	-0.776	9.27	0.325	9.29	0.327	0.021	0
		0.109	C	8.639	1.056	8.567	0.943	-0.072	9.18	0.356	9.35	0.332	0.167	0
		0.218	D	8.915	0.849	9.156	0.848	0.242	9.28	0.245	9.55	0.245	0.269	0
		0.438	E	8.460	1.021	7.852	0.945	-0.629	9.13	0.392	9.18	0.390	0.042	0
		0.875	F	8.787	1.013	8.116	0.985	-0.671	9.26	0.337	9.29	0.358	0.029	0

Note: Temperature data, i = temperatures increasing
s = temperatures steady
d = temperatures decreasing during period of experiment.

Table IX. Results of growth experiments on prey of different particle size.
(ranked in order of fish age)

Run	Mean temp. deg.C	Mean feed diameter cm	Code	Mean initial weight gm	SD	Mean final weight gm	SD	Weight change gm	Mean initial length cm	SD	Mean final length cm	SD	Length change cm	Mortality No./24
10	9.9(i)	-	A	0.168	0.011	0.178	0.005	0.010	2.85	0.051	2.92	0.059	0.071	-
		0.017	B	0.172	0.010	0.185	0.003	0.013	2.85	0.051	2.93	0.048	0.088	-
		0.033	C	0.171	0.011	0.206	0.006	0.035	2.85	0.051	2.98	0.082	0.138	-
		0.066	D	0.171	0.009	0.207	0.005	0.036	2.85	0.051	3.00	0.069	0.150	-
		0.129	E	0.169	0.012	0.202	0.007	0.034	2.85	0.051	2.97	0.104	0.121	-
		0.258	F	0.170	0.009	0.207	0.006	0.038	2.85	0.051	2.99	0.074	0.133	-
12	17.2(s)	0.017	A	0.689	0.072	0.704	0.064	0.015	4.15	0.147	4.22	0.382	0.670	3
		0.028	B	0.635	0.071	0.693	0.065	0.058	4.10	0.146	4.20	0.410	0.100	0
		0.055	C	0.680	0.086	0.803	0.072	0.123	4.14	0.162	4.35	0.463	0.209	1
		0.109	D	0.657	0.083	1.192	0.079	0.535	4.14	0.164	4.82	0.412	0.679	0
		0.218	E	0.696	0.078	1.140	0.070	0.444	4.20	0.158	4.76	0.378	0.559	7
		0.438	F	0.684	0.074	0.914	0.056	0.231	4.16	0.150	4.46	0.294	0.300	8
3	18.5(d)	0.019	A	3.322	0.442	2.851	0.369	-0.471	6.69	0.254	6.63	0.254	-0.063	0
		0.039	B	3.333	0.462	2.916	0.496	-0.417	6.73	0.291	6.64	0.313	-0.089	5
		0.078	C	3.330	0.439	3.075	0.596	-0.255	6.72	0.253	6.73	0.322	0.008	0
		0.155	D	3.249	0.412	4.448	0.525	1.199	6.67	0.272	7.30	0.249	0.639	1
		0.308	E	3.325	0.386	3.122	0.524	-0.203	6.72	0.237	6.77	0.301	0.048	1
		0.615	F	3.283	0.392	3.117	0.494	-0.166	6.65	0.257	6.74	0.312	0.087	0
5	9.3(d)	0.028	A	8.825	1.141	8.067	1.046	-0.758	9.25	0.361	9.15	0.558	-0.104	0
		0.055	B	8.895	0.982	8.118	0.890	-0.776	9.27	0.325	9.29	0.327	0.021	0
		0.109	C	8.639	1.056	8.567	0.943	-0.072	9.18	0.356	9.35	0.332	0.167	0
		0.218	D	8.915	0.849	9.156	0.848	0.242	9.28	0.245	9.55	0.245	0.269	0
		0.438	E	8.480	1.021	7.852	0.945	-0.629	9.13	0.392	9.18	0.390	0.042	0
		0.875	F	8.787	1.013	8.116	0.985	-0.671	9.26	0.337	9.29	0.358	0.029	0

Note: Temperature data, i = temperatures increasing
s = temperatures steady
d = temperatures decreasing during period of experiment.

Table IX (continued)

Run	Mean temp. deg.C	Mean feed diameter cm	Code	Mean initial weight gm	SD	Mean final weight gm	SD	Weight change gm	Mean initial length cm	SD	Mean final length cm	SD	Length change cm	Mortality No./24
7	4.4(d)	0.028	A	10.30	0.716	9.60	0.666	-0.705	9.90	0.220	9.92	0.210	0.022	1
		0.055	B	9.80	1.051	9.23	0.996	-0.579	9.70	0.396	9.75	0.367	0.046	0
		0.109	C	9.85	1.139	9.70	1.129	-0.154	9.73	0.359	9.81	0.368	0.087	0
		0.218	D	10.43	1.053	10.06	1.186	-0.363	9.88	0.297	9.98	0.372	0.100	2
		0.438	E	10.12	1.014	9.46	0.947	-0.665	9.84	0.280	9.82	0.299	-0.021	0
		0.875	F	9.61	1.027	9.04	0.965	-0.568	9.68	0.331	9.69	0.346	0.017	0
9	4.5(i)	0.033	A	12.00	1.213	10.94	1.131	-1.056	10.43	0.325	10.48	0.312	0.046	0
		0.066	B	12.22	1.096	11.23	1.021	-0.981	10.47	0.279	10.52	0.294	0.050	0
		0.129	C	12.16	1.089	11.92	1.039	-0.243	10.49	0.300	10.58	0.311	0.083	0
		0.258	D	12.47	1.013	12.41	1.001	-0.064	10.60	0.255	10.75	0.268	0.146	0
		0.518	E	12.56	1.282	11.62	1.213	-0.936	10.57	0.350	10.61	0.369	0.046	0
		1.035	F	12.38	1.136	11.55	1.093	-0.828	10.55	0.322	10.60	0.334	0.046	0
11	13.0(i)	0.023	A	6.657	0.752	5.906	0.619	-0.751	8.58	0.284	8.48	0.291	-0.100	0
		0.046	B	6.654	0.696	5.912	0.742	-0.742	8.55	0.286	8.48	0.304	-0.063	0
		0.093	C	6.649	0.626	7.237	0.900	0.588	8.60	0.249	8.85	0.266	0.246	0
		0.185	D	6.662	0.490	9.135	0.757	2.473	8.60	0.223	9.36	0.224	0.758	0
		0.368	E	6.578	0.607	7.446	0.864	0.868	8.54	0.267	8.83	0.282	0.288	0
		0.735	F	6.733	0.551	6.597	0.600	-0.135	8.58	0.247	8.66	0.245	0.083	0
4	14.1(d)	0.055	A	63.79	9.272	57.63	8.760	-6.163	17.78	0.867	17.97	0.895	0.196	1
		0.109	B	66.29	10.87	63.77	9.434	-2.520	17.95	0.820	18.34	0.886	0.383	0
		0.218	C	62.41	8.005	65.23	7.679	2.815	17.69	0.621	18.14	0.596	0.450	0
		0.438	D	57.79	5.561	63.86	7.130	6.068	17.37	0.551	17.96	0.686	0.591	1
		0.875	E	60.46	10.79	55.53	8.701	-4.928	17.54	0.888	17.80	0.872	0.259	2
		1.220	F	63.90	10.56	59.10	10.20	-4.800	17.80	0.809	17.98	0.870	0.183	0

Table IX (continued)

Run	Mean Temp. deg.C	Mean feed diameter cm	Code	Mean initial weight gm	SD	Mean final weight gm	SD	Weight change gm	Mean initial length cm	SD	Mean final length cm	SD	Length change cm	Mortality No./24
6	5.5(d)	0.055	A	96.79	11.50	92.41	11.29	-4.376	20.11	0.792	20.15	0.825	0.038	0
		0.109	B	96.60	13.55	92.32	13.15	-4.280	20.17	0.986	20.20	1.014	0.029	0
		0.218	C	95.04	9.93	94.93	9.10	-0.110	20.07	0.821	20.26	0.667	0.196	0
		0.438	D	101.61	11.12	97.72	9.74	-3.892	20.54	0.722	20.78	0.852	0.233	0
		0.875	E	100.16	11.97	94.02	11.27	-6.148	20.41	0.743	20.44	0.718	0.025	0
		1.220	F	98.04	10.37	93.32	9.54	-4.722	20.27	0.567	20.35	0.627	0.083	0
15	4.5(i)	0.039	A	26.24	1.815	24.29	1.784	-1.959	13.36	0.279	13.28	0.303	-0.075	0
		0.078	B	26.46	1.679	24.71	1.586	-1.753	13.35	0.287	13.39	0.316	0.042	0
		0.155	C	26.63	1.831	25.99	1.955	-0.643	13.39	0.290	13.50	0.305	0.113	0
		0.308	D	26.12	1.829	25.15	1.645	-0.967	13.28	0.291	13.38	0.300	0.110	0
		0.615	E	26.82	1.710	24.98	1.688	-1.839	13.43	0.311	13.43	0.298	-0.004	0
		1.22	F	27.09	1.888	25.36	1.767	-1.725	13.46	0.263	13.49	0.274	0.030	0

Table X. t-values for weight changes during experiments, and their significances.

Feed size code	A	B	C	D	E	F
Run No.						
10	3.984 P<0.001	5.991 P<0.001	13.409 P<0.001	16.822 P<0.001	11.765 P<0.001	19.289 P<0.001
12	0.698 P>0.10	2.891 P<0.01	5.261 P<0.001	22.404 P<0.001	16.999 P<0.001	9.645 P<0.001
3	3.880 P<0.001	2.616 P<0.02	1.653 P>0.10	8.619 P<0.001	1.495 P>0.10	1.263 P>0.10
5	2.349 P<0.05	2.809 P<0.01	0.244 P>0.10	0.968 P>0.10	2.169 P<0.05	2.278 P<0.02
7	3.459 P<0.01	1.918 P<0.10	0.461 P>0.10	1.098 P<0.10	2.299 P<0.05	1.937 P<0.10
9	3.055 P<0.01	3.142 P<0.01	0.774 P>0.10	0.216 P>0.10	2.544 P<0.02	2.520 P<0.02
11	3.699 P<0.002	3.498 P<0.002	2.573 P<0.02	13.156 P<0.001	3.944 P<0.001	0.795 P>0.10
4	2.318 P<0.05	0.839 P<0.10	1.218 P>0.10	3.219 P<0.01	1.706 P<0.10	1.568 P>0.10
6	1.302 P>0.10	1.089 P>0.10	0.039 P>0.10	1.263 P>0.10	1.794 P<0.10	2.375 P<0.05
15	3.691 P<0.002	3.640 P<0.002	1.151 P>0.10	1.885 P<0.10	3.717 P<0.002	3.199 P<0.01

FIGS 5-14. Growth response to prey size.

Legend:

—   W%   Change in weight over 20 days as percent initial weight

---   l%   Change in length over 20 days as percent initial length

       PFR   Ratio of mean prey diameter: mean fish length

       Temperature regime during experimental run:

            (i)   increasing
            (s)   steady
            (d)   decreasing

NB: Value of P (t-test, Table X) indicated adjacent to each point

Fig 5   Run 10   L - 2.9cm   Temp. 9.9°C (i)

Fig 5   Run 10   L - 2.9cm   Temp. 9.9°C (i)
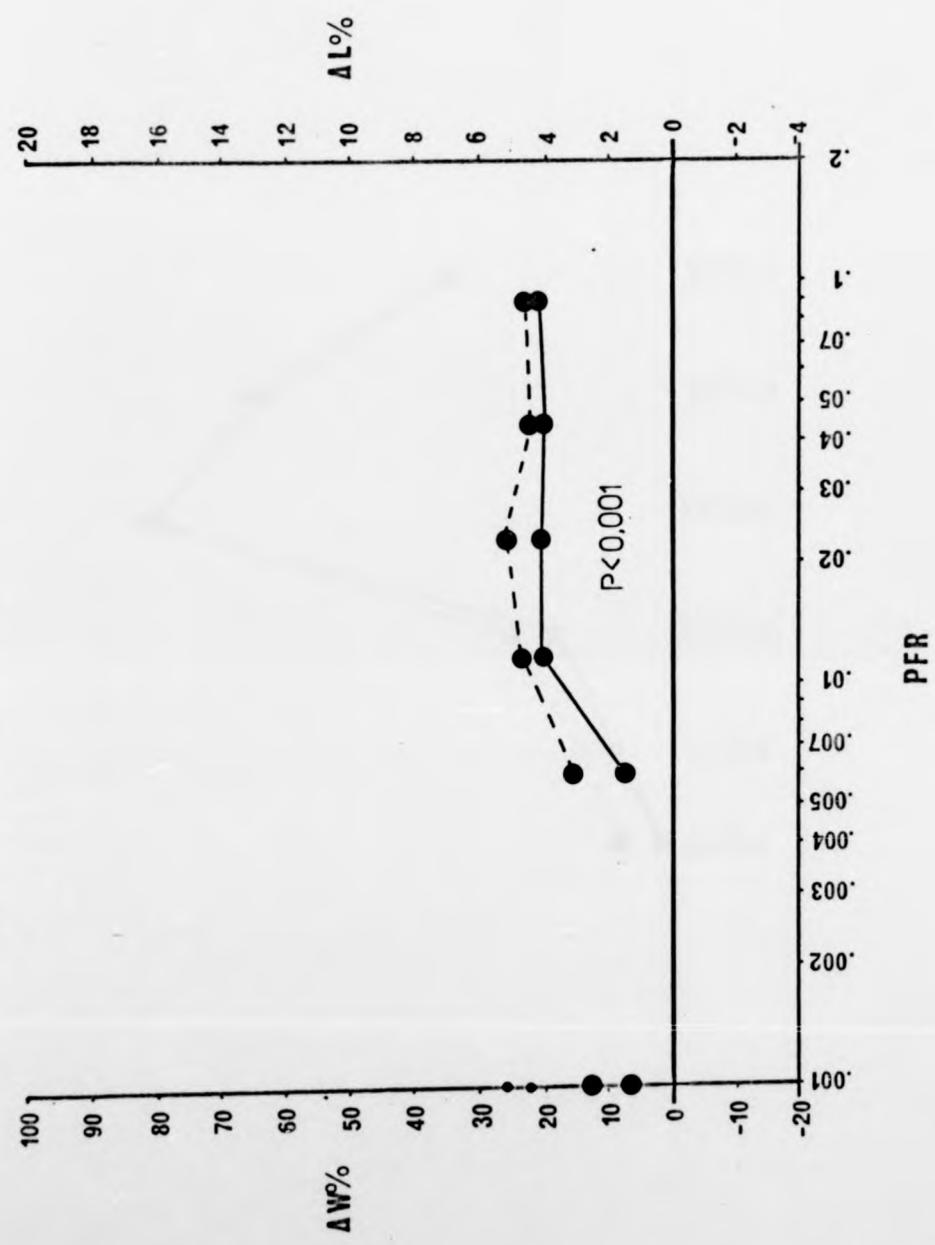
Fig 6   Run 12   L - 4.2cm   Temp. 17.2°C (s)
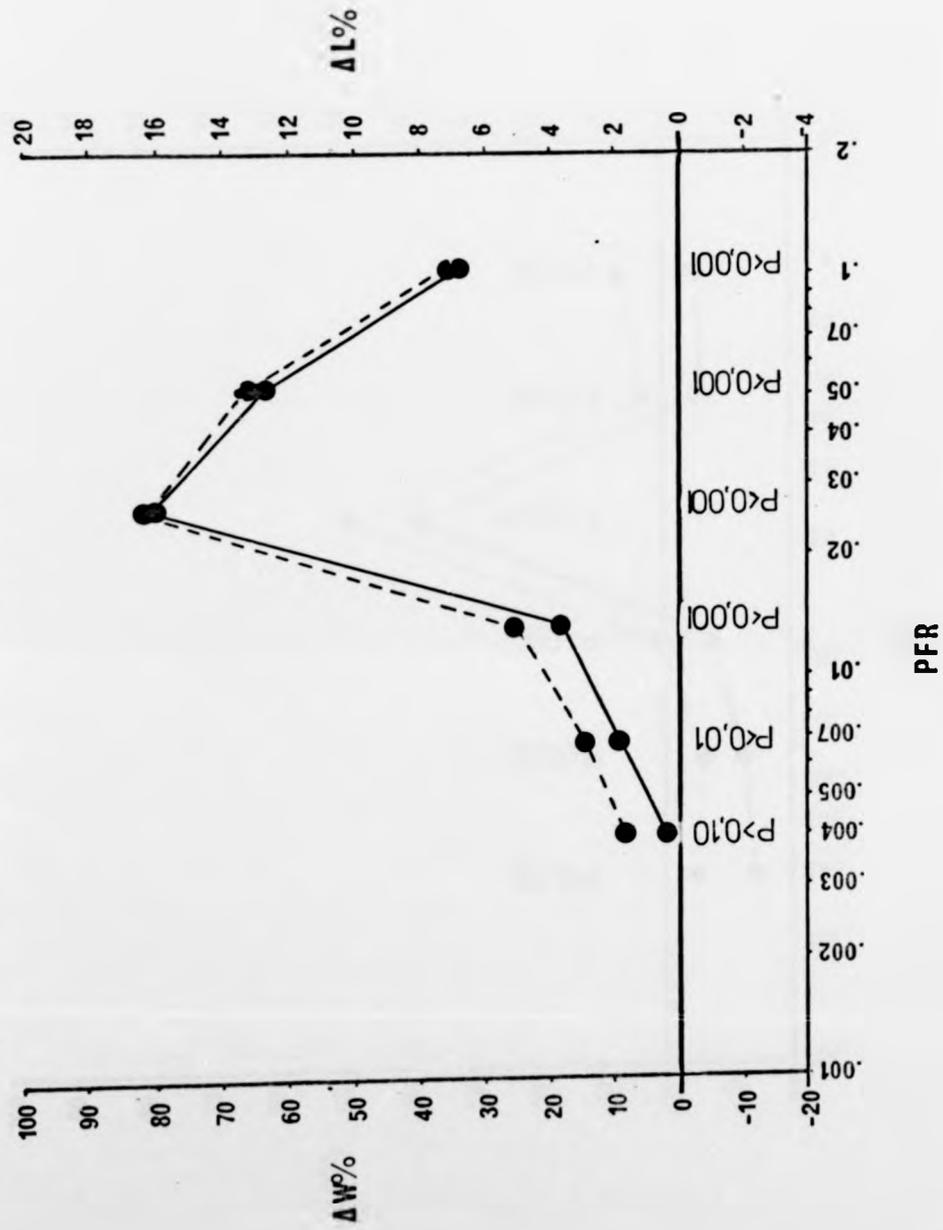
Fig 7   Run 3   L - 6.7cm   Temp. 185° C (d)
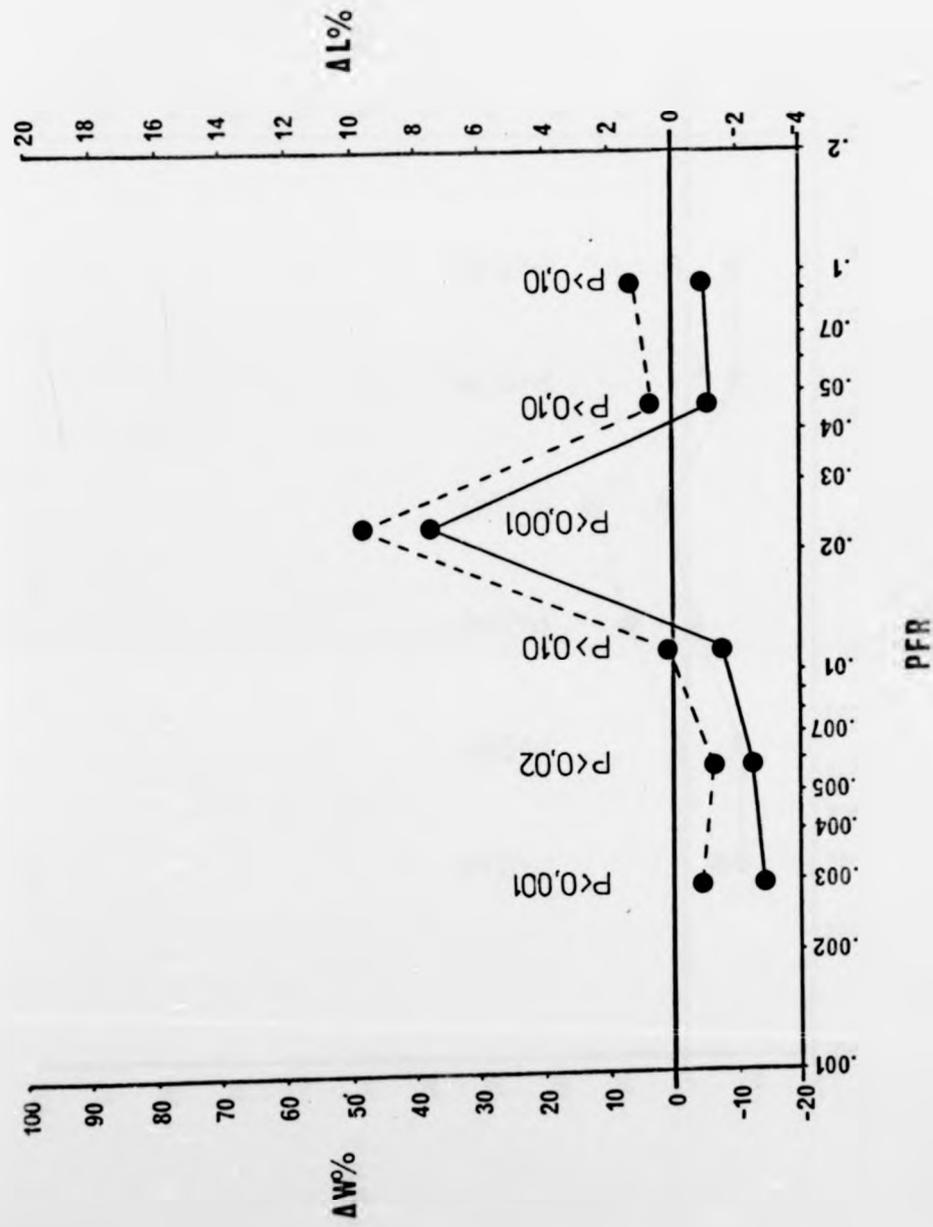
Fig 8   Run 5   L-9.2cm   Temp. 9.3°C (d)
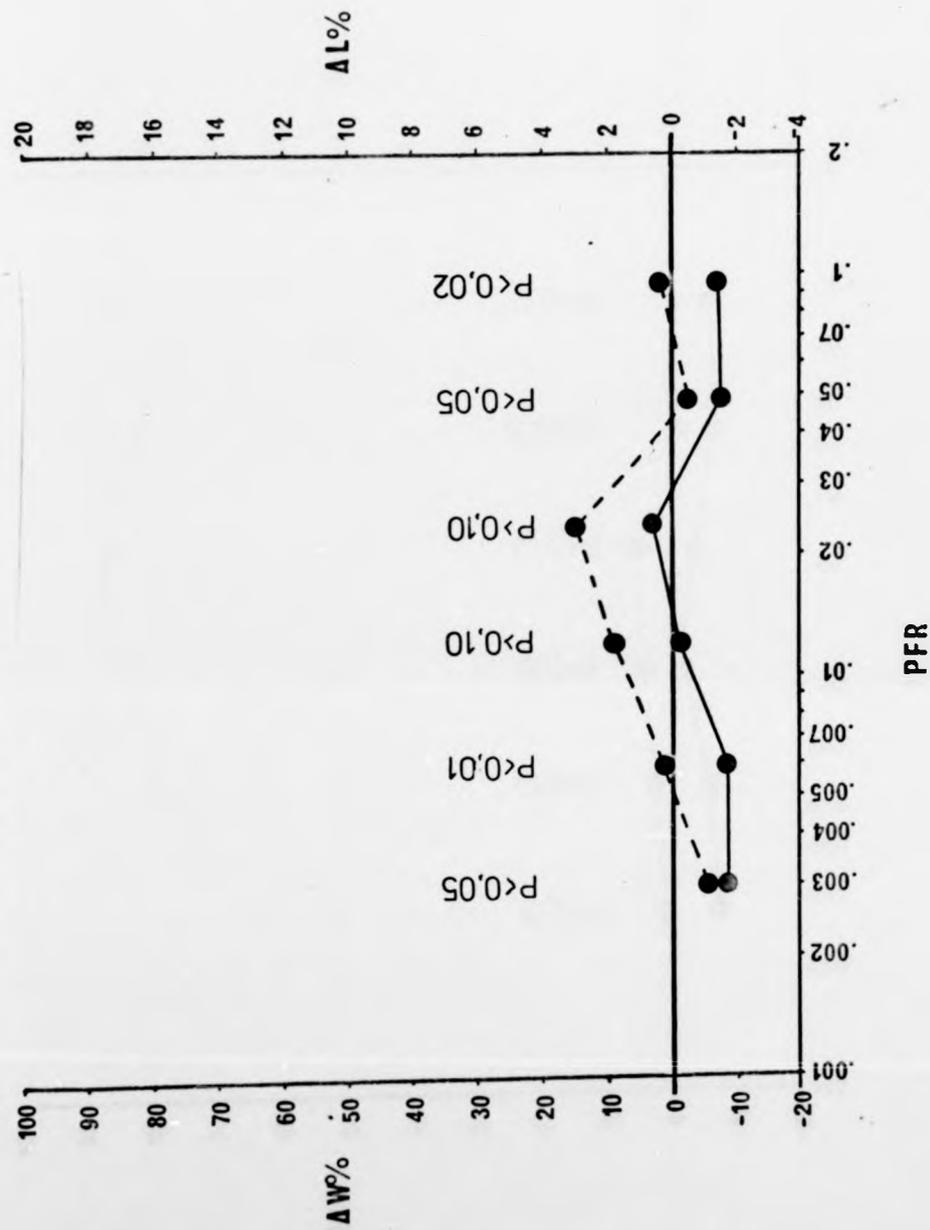
Fig 8   Run 5   L - 9.2 cm   Temp. 9.3°C (d)
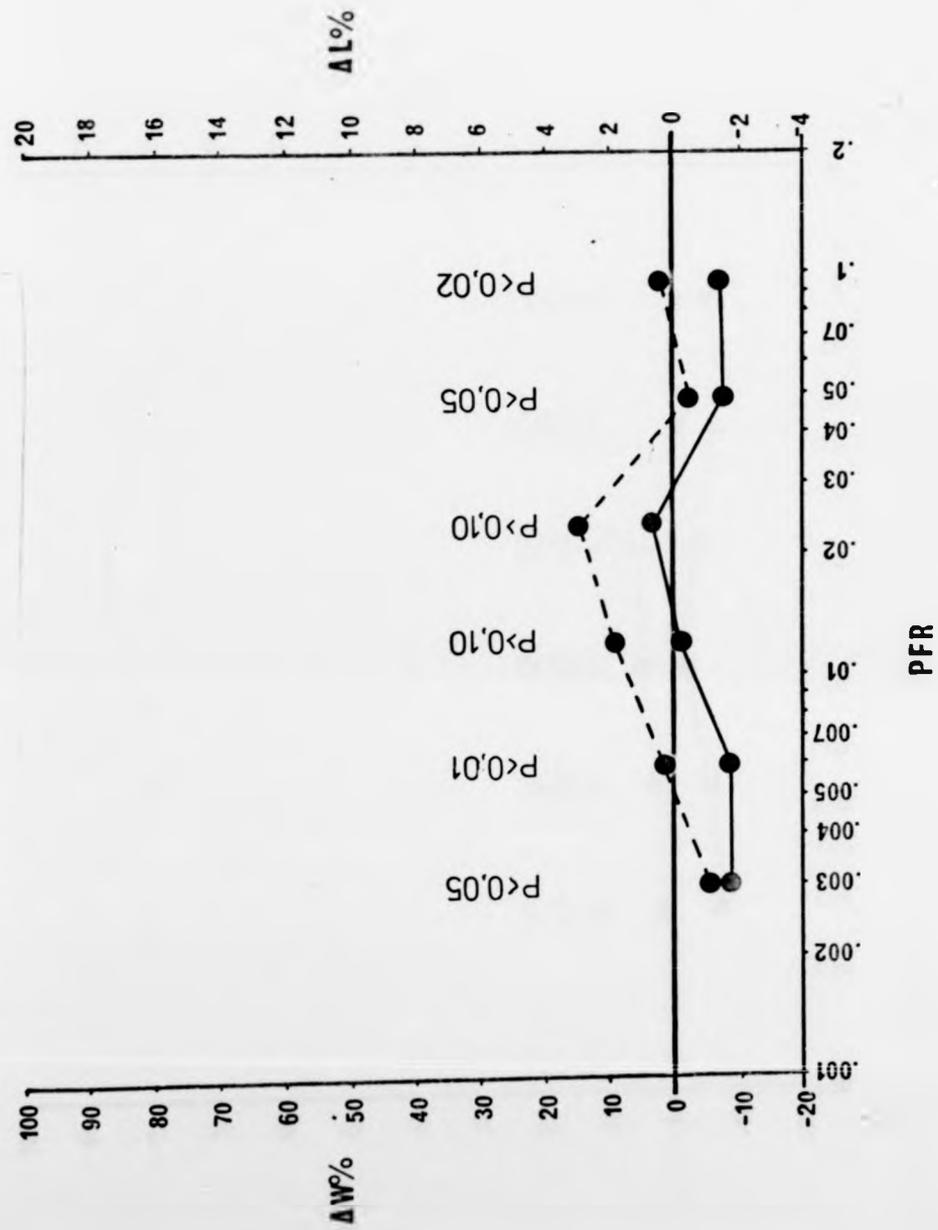
Fig 9   Run 7   L-9.8cm   Temp. 4.4°C (d)
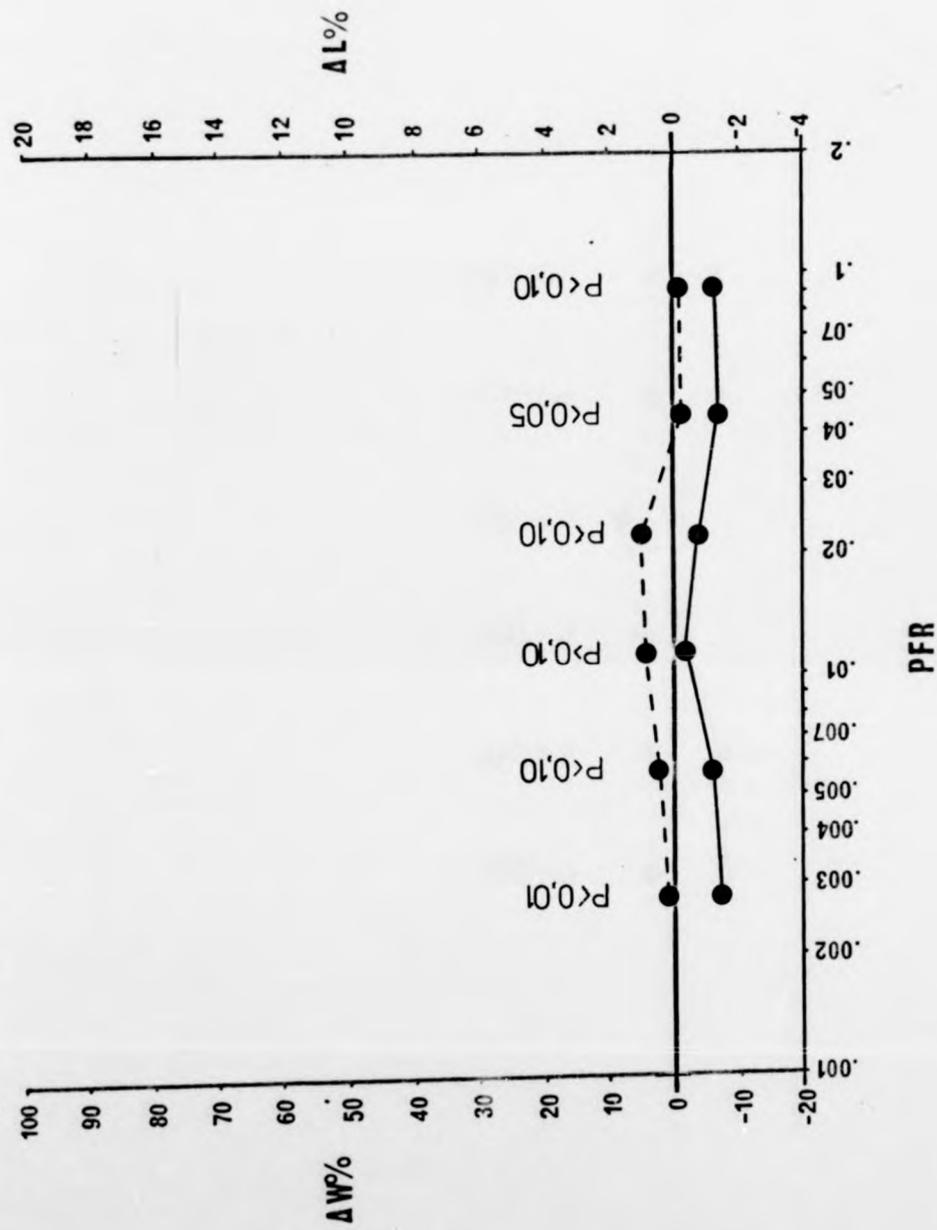
Fig 10   Run 9.   L - 10.5 cm   Temp. 4.5°C (i)

ΔL%

PFR

ΔW%

P<0.02   P<0.02   P>0.10   P>0.10   P<0.01   P<0.01
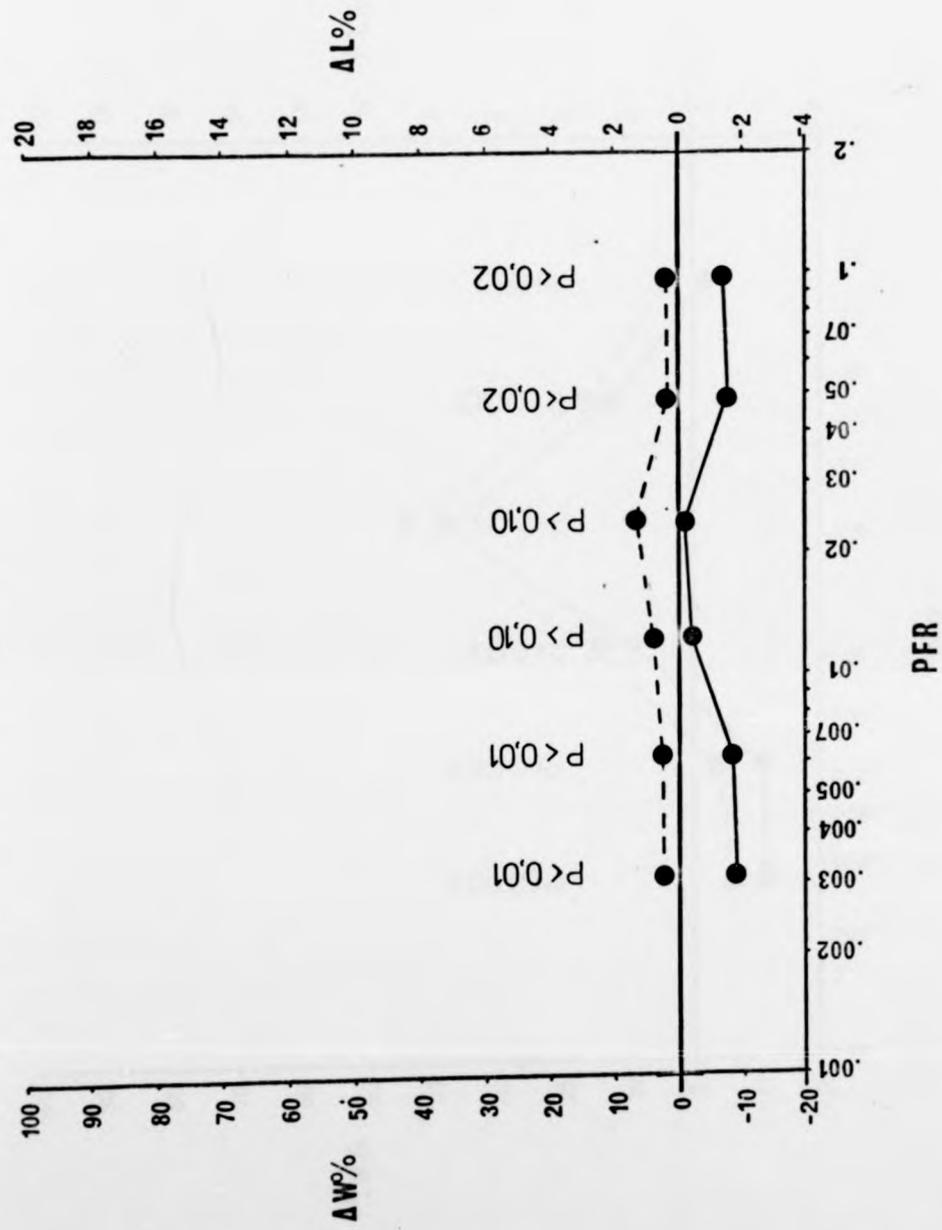
Fig 11   Run 11   L - 8.6 cm   Temp. 13.0°C (i)
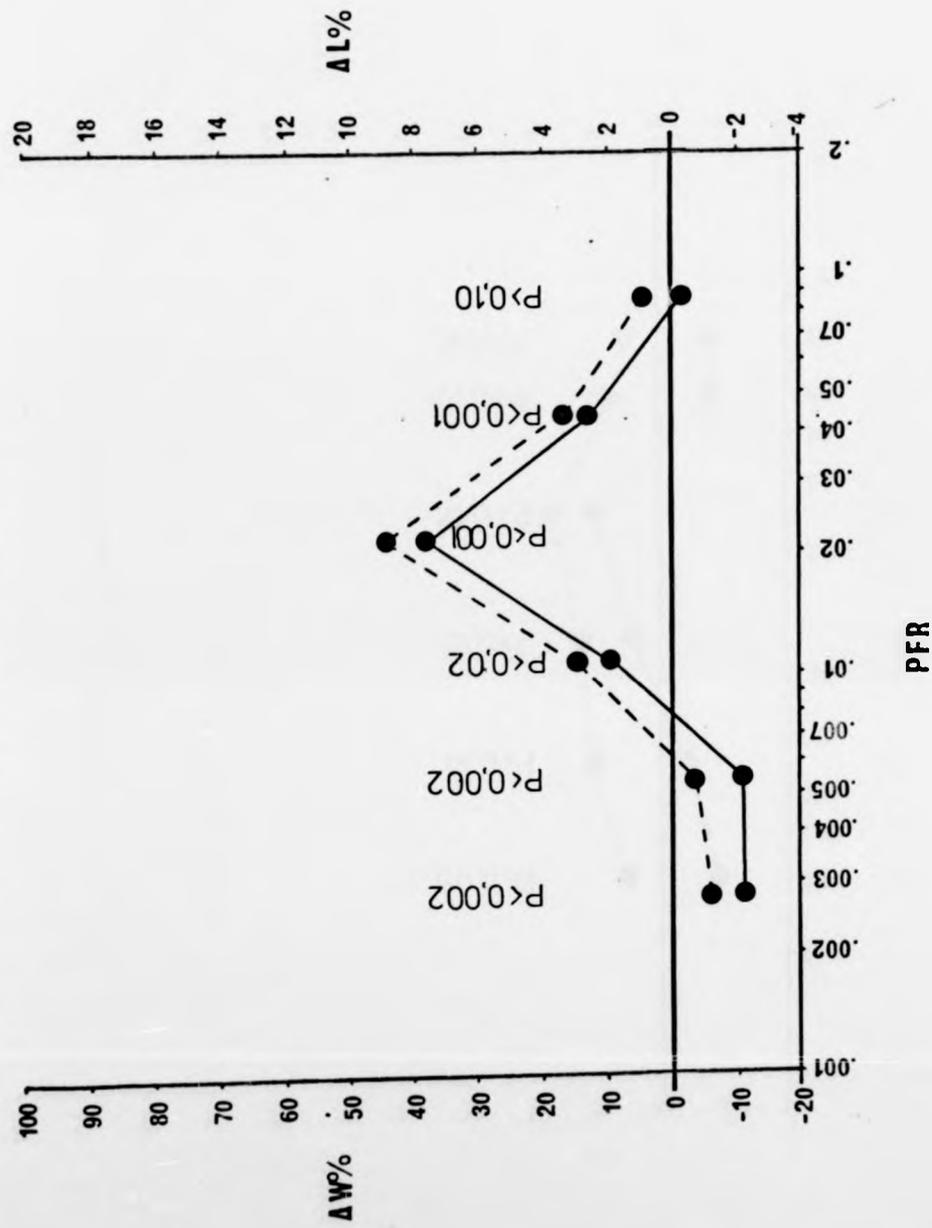
Fig 12   Run 4   L – 17.7cm   Temp. 14.1°C(d)

Fig 13   Run 6   L - 20.3 cm   Temp. 5.5°C (d)
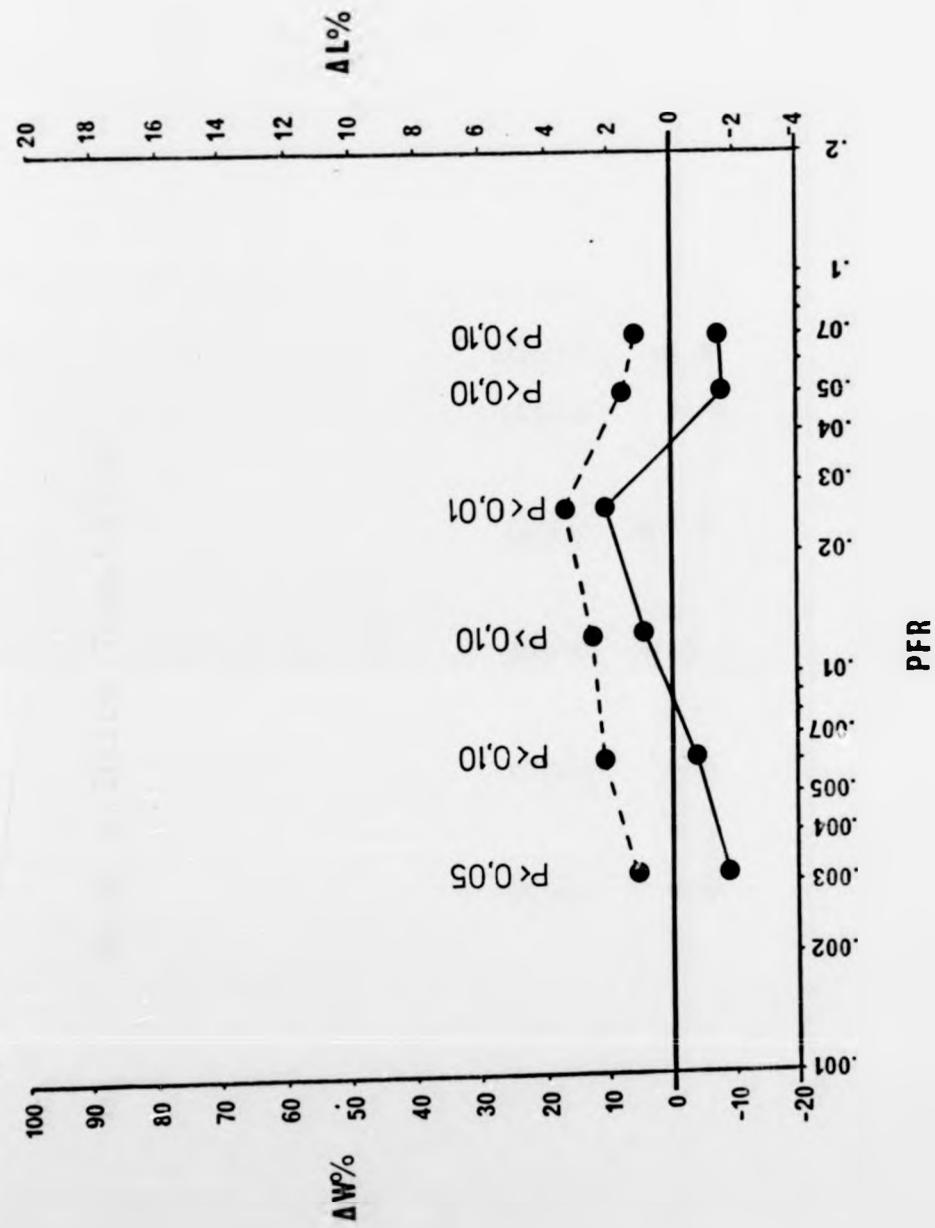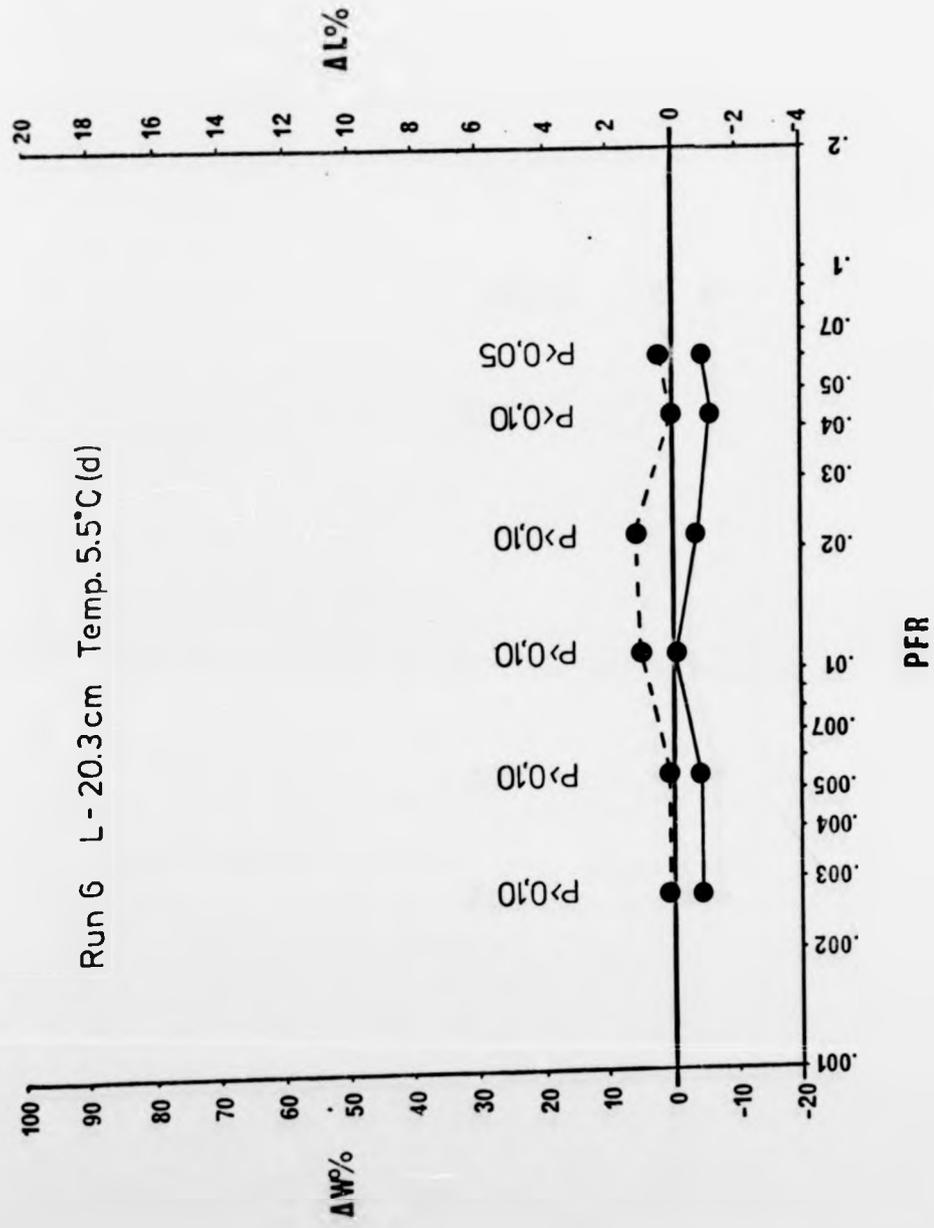
Fig 14   Run 15   L - 13.4 cm   Temp. 4.5°C (i)
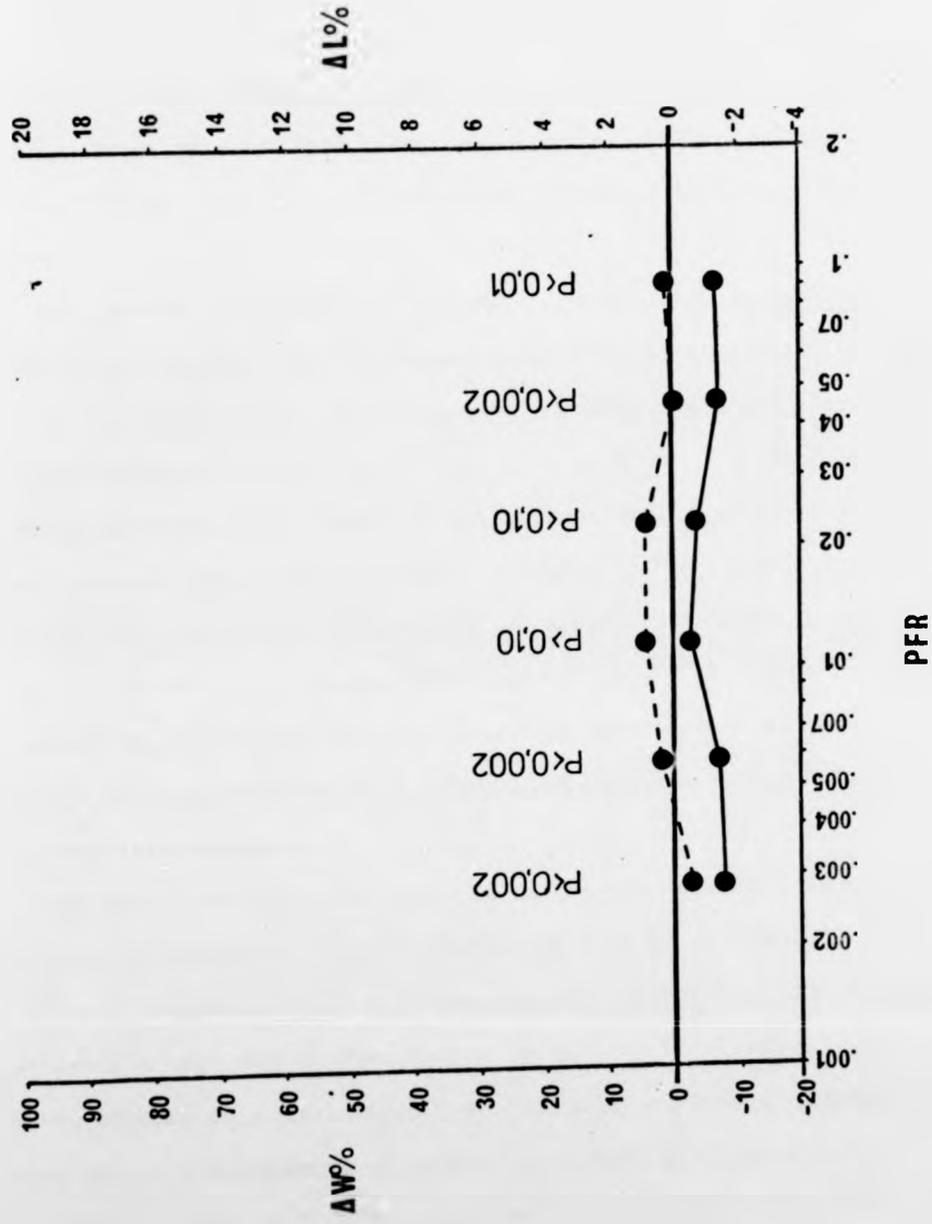
Fig 14   Run 15   L - 13.4 cm   Temp. 4.5°C (i)
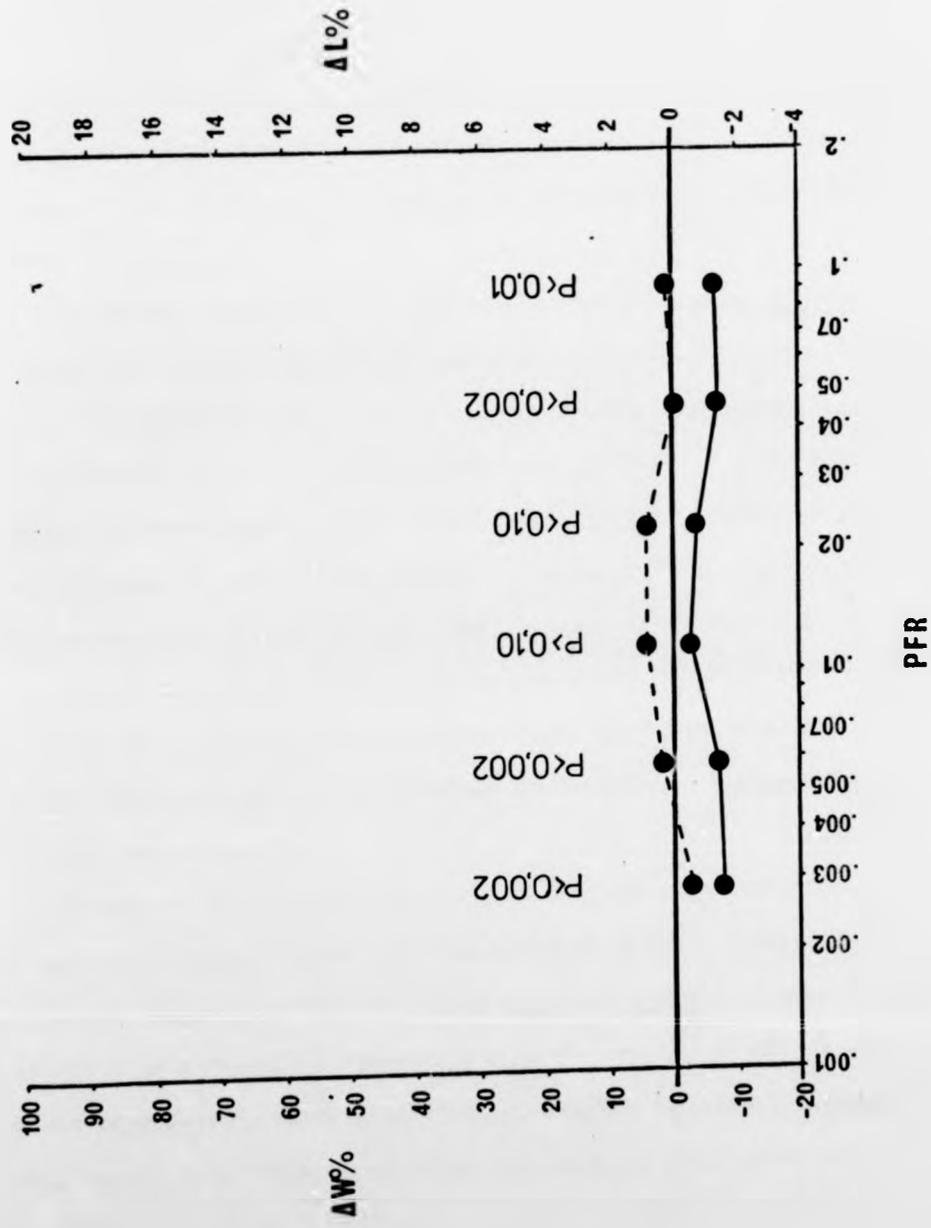
DISCUSSION

The growth of fish may be affected by a number of often closely related factors (e.g. genetic origin, social interactions, ration level, water temperature). Although within each experimental run all but prey size were eliminated as variables between tanks this was not the case between runs, and it is therefore pertinent to examine these factors.

The genetic origin of fish influences growth (Thorpe, pers.comm [*]) and since four separate family groups, each of different genetic origin although all from the same river system stock (Tay), were used during the experimental series it follows that care needs to be taken when comparing absolute growth rates between experiments. However as peak growth response occured at the same prey diameter: fish length ratio (relative prey size, P.F.R.)(Table IX) irrespective of family group and as the general relationship between growth and P.F.R. (Figs 5 - 14) was common to all groups, it is unlikely that the relative effect of prey size was influenced by differences in the genetic background of stock fish between runs.

The effect of social interactions on the growth of individual fish within a population has been demonstrated by Brown (1946, 1) in brown trout, Magnuson (1962) in Medaka (Oryzias latipes), Symons (1971) in Atlantic salmon, all of whom found that the growth of subordinate fish was repressed by dominants. The opportunity for social interactions leading to the establishment of social hierarchies and, under certain conditions, to overt territoriality by dominant fish was reduced by the provision of cover within tanks. Thus, although it is unlikely

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[*] Genetic control of growth in juvenile salmon has been demonstrated unequivocally in recent experiments at Almondbank. In a half-sib mating design, variation in the length of progeny was analysed at 6 months after hatching, and significant ($p < 0.01$) differences in size were demonstrated between the progeny of individual parents, the female parent apparently influencing absolute size, while the male influenced developmental rate.

that agonistic encounters were entirely suppressed, the use of cover resulted in the establishment of a fish distribution which encouraged maximal feeding opportunity for all fish within one tank, and good correspondence was shown between tanks. The provision of cover directly related to fish size-class had the additional advantage that relative available feeding space per fish beneath cover remained constant between size-classes.

Results are presented as growth over the period of the experiment (20 days) as the use of Specific Growth Rate as a measure of performance has been avoided since it implies a constant growth rate throughout the period of each experiment. As fish were stressed at the commencement of each experimental run by transference to an unfamiliar environment, starvation, anaesthesia and subsequent maltreatment in the course of weighing and measuring it is unlikely that normal feeding patterns and growth would have been resumed immediately, precluding the establishment of a constant growth rate.

It is possible that poor overall performance at low temperatures occured partly as a result of the longer term effect of pre-experimental stress as the time required to make up energy losses would be extended at lower temperatures (Elliott 1976).

The effect of prey size on growth in weight and growth in length was directly comparable in all cases except runs 6, 7 and 15. In run 6 growth in weight was shown at a P.F.R. of 0.011 and in length at 0.022, and in runs 7 and 15 in weight at 0.011 and 0.012 and length at both 0.011 - 0.012 and 0.022 - 0.023. In the case of runs 6 and 7 this occurred as temperatures were dropping to a minimum winter level (means 5.5 and 4.4 degrees C at the end of November and December respectively) and in two age classes of fish (1+;20.3 cm, and 0+;9.8 cm). Although neither weight change was statistically significant the characteristic form of the prey size/growth curve common to all other runs was otherwise retained. Run 15 was a similar case although at the end of the winter

season(4.5 degrees C during March, 1+;13.4 cm fish). In the following discussion no distinction will generally be made between growth in weight and in length.

The existence of a prey size related growth rate was clearly demonstrated. Optimum prey size occurred at a P.F.R. of about 0.022 - 0.026 and well within the range delimited by 0.011 and 0.052 during most of the year. Therefore, since the P.F.R. remained constant, the optimum prey size increased in direct proportion to fish length. An increase (not necessarily proportional) in optimum prey size with fish growth has been predicted by Paloheimo and Dickie (1965 and 1966) from their model of fish growth. Their exponents governing growth efficiency are dependant on energy expenditures during grazing and their integration with the success of food acquisition, on which prey size appears to exert the predominant effect. A similar prediction was made by Kerr whose model (1971, 2) implies that sustained growth requires increasingly large prey sizes, even if rare.

The bias shown towards good growth on prey larger and smaller than 0.022 - 0.026 P.F.R. during June, July and September, October respectively implies flexibility of response to prey size. The months of June and July are periods of characteristically rapid growth in salmonids during the early part of the growth season (Brown 1946, 2, Swift 1961, Allen 1969) and therefore maximisation of food consumption would be expected at this time of year. Since it is possible that consumption may be enhanced by the use of larger prey (Elliott 1975, 3) and since the weight (thus energy content) of prey of P.F.R. 0.044 is 8.0 times that of prey of 0.022 the implied disadvantages of capture and ingestion of the larger prey may in part be outweighed by the potential energy gain. September-October is a period during which growth is rapidly declining (Wingfield 1940, Brown 1946, 2) as a function of decreasing water temperatures (Elliott 1975, I and 1976) and also, in sockeye salmon at least, a seasonally induced growth check independent

of temperature (Brett et al 1969). Since this growth check occurs
independently of ration (Brett et al 1969, Elliott 1975, I) it follows
that consumption and, within reason, prey accessibility may no longer
be critical factors at this time of year, and a wider range of prey
sizes may in part fulfil the fish's reduced energy requirements. This
trend towards adequate use of smaller prey sizes during autumn continued
into the winter at which time peak growth in weight occured at a P.F.R.
of 0.011 (as compared to 0.022 - 0.026 during the summer) in both age
classes of fish. Recalculation of data from Allen (1940 and 1941) shows
that in Atlantic salmon populations in the River Eden there is a
similar progression of decrease in mean relative prey size from early
summer to autumn (table XI).

A number of factors (Table XII) are likely to affect the net energy
gain for growth resulting from feeding on a variety of prey particle
sizes. Clearly the energy content of prey items differing only in size
decreases with decreasing weight which under the experimental conditions
was by a factor of 8.0 between sizes (1, Table XII). Since it is
reasonable to assume that energy expenditure during capture (excluding
search and ingestion) remains independent of prey size the net energy
gain per unit of energy acquired must decrease with decreasing prey
size (2). The number of prey available during one feeding period
increased exponentially with prey size decrease (Fig. 15). Since a
negatively exponential relationship between size and density is a
characteristic feature of animal populations (MacArthur 1972) this is
therefore also likely to apply to naturally available prey. As larger
prey are rare (3) feeding opportunity decreases and the success of
capture and ingestion (5) becomes critical. Paradoxically more time
would therefore be available for post-capture manipulations and energy
losses during their course may be of little consequence (4). Increase
in feeding opportunity with more numerous smaller prey and the likelihood
of successful ingestion (3 and 5) are factors acting to oppose the

Table XI. Relationship between mean fish and mean prey length in the River Eden.

Sources: Allen 1940 (Fig. 4) and 1941 (Table 3).

Fish age	Mean fish length cm.	Mean prey length cm.	Prey length*: fish length ratio	Month
0+	4.0	0.272	0.069	June
	5.0	0.302	0.060	July
	7.5	0.332	0.044	September
1+	7.5	0.447	0.060	April-May
	10.5	0.461	0.044	June
	13.0	0.453	0.035	August

Note * Since most natural prey are elongate this term is not synonymous with the term prey diameter used throughout.

FIG. 15. Variation in number of particles in 1 gm of feed with prey particle size.

Prey diameter (cm)
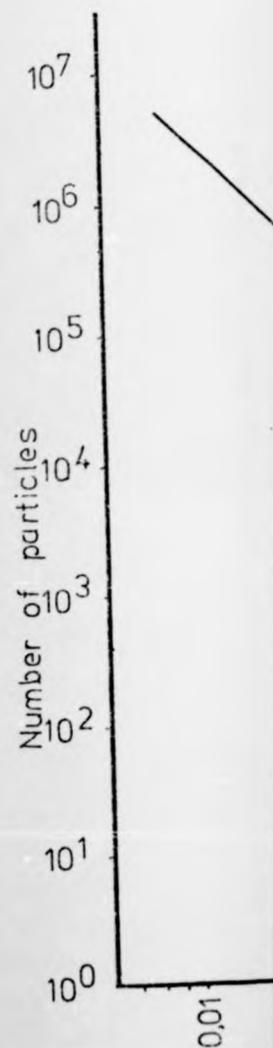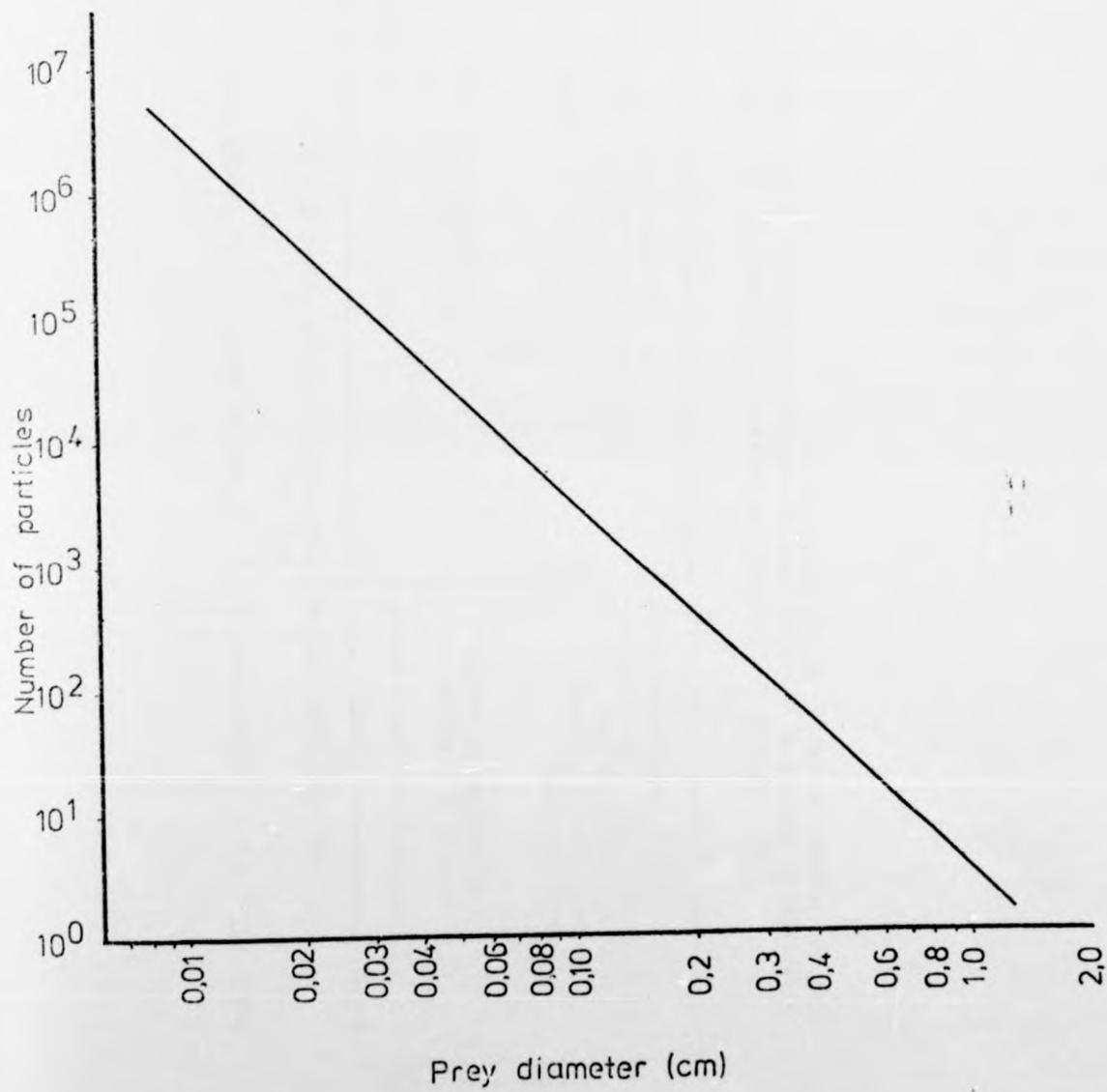
Table XII. Major factors potentially influencing growth on different prey sizes.

MAXIMUM THRESHOLD SIZE

SMALLER THAN OPTIMUM	OPTIMUM PREY SIZE	LARGER THAN OPTIMUM
1) Each item has lower energy content 2) more energy expended in acquiring a particular amount of energy. But: 3) more numerous 4) less time and energy potentially required for manipulations prior to ingestion 5) unlikely to be rejected		1) Each item has higher energy content 2) less energy expended in acquiring a particular amount of energy. But: 3) rarer 4) more time and energy potentially required for manipulations prior to ingestion 5) may be rejected

MINIMUM THRESHOLD SIZE*

*In addition a point will be reached where the cost in acquiring a prey item exceeds the energy gained. This is especially likely at higher temperatures due to elevated metabolic and activity levels.

disadvantages of (1) and (2).

Since metabolic and activity levels are temperature dependent (Winberg 1956, Warren and Davies 1966, Brett 1970, Brett and Glass 1973, Elliott 1976) the energy cost of acquiring an item may be less significant at lower temperatures while thedecreased feeding opportunity on larger, rarer items may become of crucial importance. Hence a shift in net energy intake, thus potential for growth, from larger prey at higher temperatures to smaller prey at lower. However Egglishaw (1967) reports that in the Shelligan burn the size distribution of the bottom fauna shifts progressively towards the small end of the spectrum from May to September, and since stomach contents in this case indicated feeding on material of benthic origin it may be that the above results merely indicate an adaptation to the prey that is normally available.

Clearly there must be threshold sizes outside of which prey cannot be captured, retained or ingested. This is particularly true at the upper size threshold since from observations, salmon ingest prey whole and do not bite pieces out of large particles. At the lower end of the prey size spectrum an additional limit must exist at which the mean energy expended in capture, ingestion and digestion of an item is equal to the useful energy content above that of the fish's metabolic requirements. At this level only the maintenance requirements (Brett et al 1969, Elliott 1975, II) of the fish are being met and any further decrease in prey size will consequently result in loss of weight.

Grassle (1957) found that food pellets of a P.F.R. of 0.0192 gave a faster weight recovery of rainbow and brook trout of mean length 12.5 cm than pellets of 0.0256 P.F.R. However these were given to fish previously fed only live prey and the smaller size may have enhanced behavioural accessibility. Fowler and Burrows (1971) based feed size recommendations for Chinook salmon on observation of acceptance and rejection behaviour. Their results indicate that relative prey size for this species must increase in proportion to fish size, from a P.F.R. of 0.020 at 4 cm to 0.031 at

10.5 cm. However as reported elsewhere (Chapters 2 and 3) feeding behaviour involves a complex of factors, and the study of only one may fail to give the complete picture.

Observations of alevin behaviour indicate that the capture of particulate material irrespective of its size and composition is characteristic of the initial stages of feeding (see also Allen 1941). Alevins attempt to capture any moving particle of which a large proportion of that of apparently organic origin is not rejected. Ingestion is attempted on all such retained particles with the result that an occassional cause of death at this stage is due to choking on items too large to swallow. The manipulation of such material may result in eventual intake as a result of particle break-up or the distension of jaw and oesophagus to permit ingestion. Furthermore it is possible that in thepresent experiments, due to the ration recommendations used, food at this stage was presented in excess in comparison to the restricted ration available to older fish, and may have masked prey size related differential growth. Since feeding opportunity may have been enhanced both in this way and by the use of 100 fish per tank (in comparison to 24 for all other experimental runs) it may not be justifiable to directly compare these results (Fig. 5) with others. Furthermore it should be noted that first feeding alevins presented with no additional food (category A, Table VII a) showed a significant growth in weight of 6.5% (Fig 5) indicating a contribution by naturally occuring food items in the input water flow to the overall growth of this stage.

CONCLUSIONS.

1) Growth rate was found to be closely related to prey size. Maximum growth rate was shown only on one size of prey particle, termed the optimum prey size. Prey sizes larger and smaller than optimum size resulted in a reduced growth rate, and often a loss in weight.

2) Optimum prey size increased in direct proportion to fish length.

3) The prey diameter: fish length ratio (I.F.R., an index of relative prey size) for the optimal prey size was 0.022-0.026 during most of the year, but 0.011 and 0.022 for growth in weight and length respectively during the winter.

4) At the commencement of the growth season larger prey than optimum elicited a good growth rate, fish on smaller prey did poorly. In the autumn this trend was reversed although optimum prey size still remained the same at 0.022 - 0.026 I.F.R.

5) First-feeding alevins, in contrast, showed a wide range of acceptable prey sizes, P.F.R.s of 0.011 to 0.088 eliciting comparable growth rates, poor growth being shown only on smaller sizes.

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Chapter 5

SYNTHESIS OF RESULTS

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Fig. 1 summarise the results of the effect of prey size on the visual feeding behaviour, selectivity, and growth rate taken from Chapters 2, 3 and 4 respectively. Prey size is expressed in relative terms as the Prey diameter:Fish length Ratio (P.F.R.). All results are directly comparable since all were obtained in June using 1+ fish of mean length 8.6 cm. In Chapter 3 the hypothesis was proposed that size-related prey intake was governed by mouth breadth and gill raker spacing, since these respectively limit the maximum size that can be taken into, and the minimum prey size that can be retained in the buccal cavity. However this does not mean to imply that within the prey size range so defined prey size-related differential growth does not occur, but merely that items outside these limits are effectively inaccessible. These limits (for 8.6 cm fish) are indicated in   Fig 1 (expressed as percent mean body length). As can be seen feeding behaviour closely paralleled growth response. If the prey size at which the maximum growth rate was shown is designated the optimum prey size than response to larger and smaller sizes can be considered.

Both frontal reaction and striking distances reached a maximum at a prey size closely corresponding to the optimum at which size prey acceptance also reached a near maximum. Although the proportion of available prey that was ingested remained at 100% for prey smaller than optimum the striking distance decreased. A reduction in striking distance decreases availability in proportion to the reduction of the area within which prey can be captured. With prey of P.F.R. 0.018 to 0.026 this reduction was proportional to that expected on the basis of visual mechanics alone (Cf. response distance, Fig. 1) but below 0.018 striking distance decreased far more rapidly than vision would account for. Thus fish showed negative selection for prey smaller than 0.018 P.F.R., and if the trend is extrapolated then prey of a P.F.R. of 0.0115 would represent

FIG 1. Feeding behaviour, selection and growth

Top   -   Response, reaction and strike distances
            (June, 8.6 cm fish)

            R_r - response distance
            R_a - frontal reaction distance
            S   - striking distance

Middle - Selectivity (June, 8.6 cm fish)

Bottom - Growth (Run 11, June, 8.6 cm fish)

            W% - percent change in weight
            l% - percent change in length
            FFR - prey diameter: fish length ratio

M.G.R. - Mean gill raker spacing (8.6 cm fish)
M.M.B. - Mean mouth breadth (8.6 cm fish)
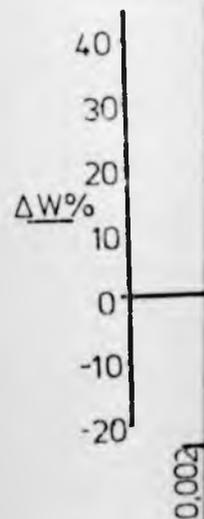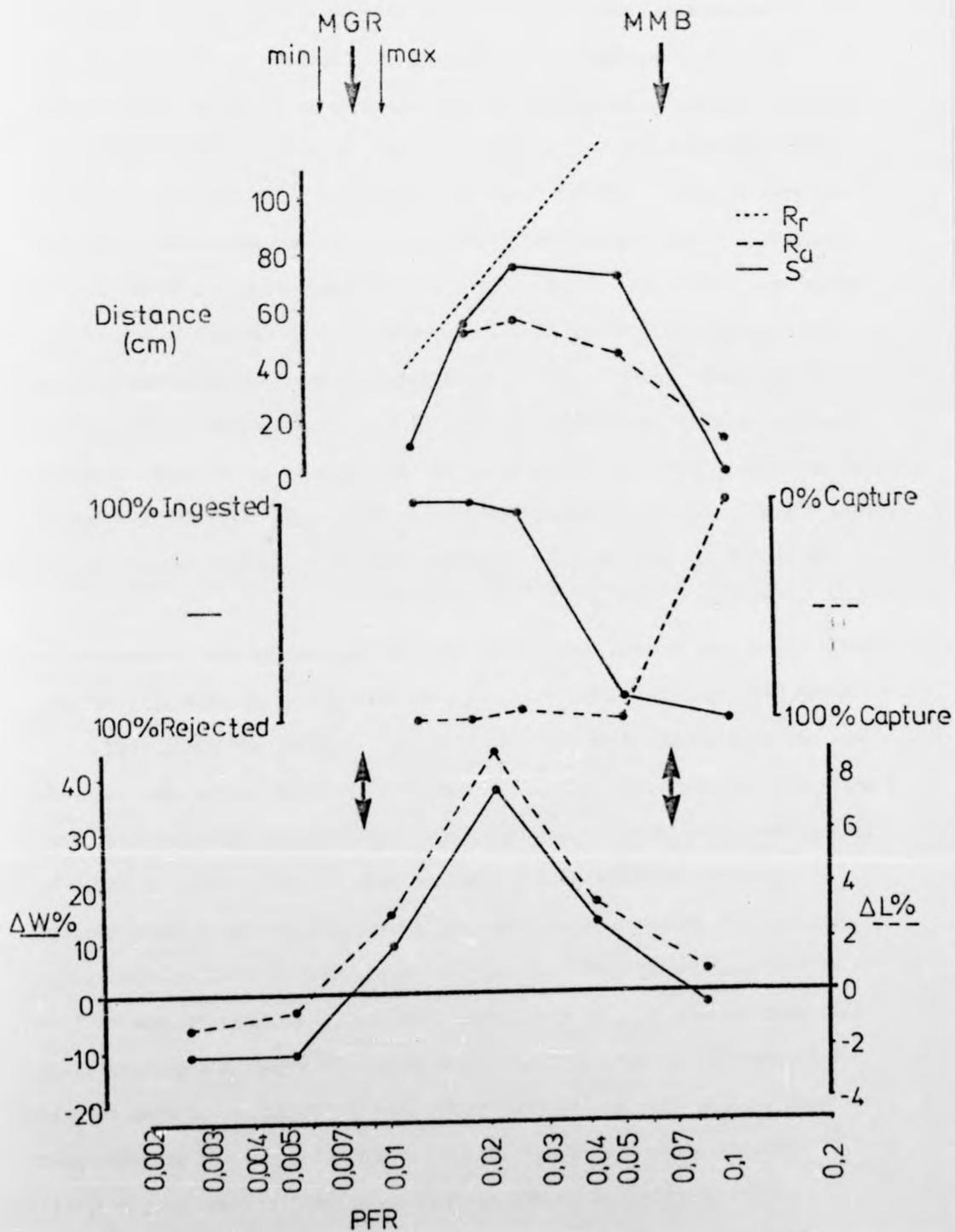
the minimum size which would be captured. This corresponds closely with the raker spacing in fish of this size, although this correspondence may well be fortuitous. Growth rate dropped to zero between 0.0108 and 0.0054 P.F.R. as would be expected from consideration of feeding behaviour.

Fish feeding on larger prey than optimum size retained comparable reaction and strike distances up to a P.F.R. of 0.051. However over the same size range acceptance-rejection behaviour changed from a rejection of only 4% of available prey to a rejection of 90%. Over this size range the weight of individual prey increases 8-fold, hence fewer larger prey would benecessary to provide a particular weight of food, which may explain ` why the growth rate on 0.042 P.F.R. prey was maintained at about 0.35 of maximum. However taking into account the prey size related complex of feeding energy expenditures (Chapter 4) no simple relationship between weight intake and growth can at this stage be formulated. Between prey of P.F.R. of 0.051 and 0.102 the proportion of available prey captured dropped to zero, corresponding with an increase in prey diameter to larger than mouth breadth and the reduction in growth rate to a negative value between 0.042 and 0.0^{0}4.

Throughout the juvenile period of the life-cycle maximum growth was shown on prey of a P.F.R. of 0.022-0.026, although there was an indication that this response was seasonally variable. Good growth was shown on prey of 0.022 to 0.044 P.F.R. in June and July but the maximum response progressively decreased throughout the summer and autumn to a P.F.R. of approximately 0.011 in mid-winter (Chapter 4). Fish in therange 6.7 to 20.3 cm consistently showed maximum weight loss on prey smaller than mean raker spacing and larger than mean mouth breadth. 4.2 cm fish showed a minimum gain in weight (of 0.12-0.024 of maximum) on prey smaller than raker spacing but 0.41 of maximum on prey larger than mouth breadth. 2.8 cm fish, on prey smaller than raker spacing, showed a change in weight comparable to starved fish, although growth on prey larger than mouth breadth was equal to maximum. Since growth rate on intermediate prey sizes varied seasonally it is considered that mean mouth breadth and gill raker

spacing represent consistent morphological thresholds to the accessible
prey size spectrum up to and including smolts (with the possible exception
of first-feeding alevins), although secondary effects (e.g. temperature-
related metabolic demands and expenditures, Chapter 4) may further reduce
the useful prey size range at different times of the year. Fig. 2
indicates these absolute prey size limits and their relationship to the
optimum prey size.

Since one must assume a feeding pattern closely adapted to the prey
requirements of fish throughout the year reflected in their growth response
to different prey (otherwise experimental correspondence would need to
be regarded as purely coincidental) the, admittedly seasonally restricted,
behavioural data may be extrapolated to cover the entire year on the basis
of the growth and morphometric data alone. In which case the feeding
behaviour response to relative prey size (P.F.R.) remains the same
irrespective of fish size and it is unnecessary to postulate a shift in
selectivity towards smaller prey sizes from spring to winter as the
decrease in the reaction distance to optimal prey in autumn (Chapter 2) may
effectively reduce, if not completely eliminate, negative selection for
smaller prey sizes above the lower threshold (Fig. 1), thereby increasing
the range of maximally selected prey sizes in this direction.

Although no experiments have been conducted using natural prey in
order to verify these results for fish in the wild environment a
re-analysis of a comprehensive stomach - contents analysis study
(Egglishaw 1967) is presented in the Appendix. Although stomach-contents
analyses, for reasons given elsewhere (p. 100), should be treated with
caution it is instructive that agreement between selection of simple
artificial prey and natural prey selection (as indicated by stomach content
composition) can be demonstrated. It is nevertheless felt that
experimental verification of natural prey size selectivity would be of value,
and, since optimal prey breadth (as the P.F.R.) is now known, should
present fewer problems than previously. Within the field of aquaculture

FIG 2. Mouth breadth, gill raker spacing
and optimum prey size.

● Maximum growth in weight and
length where the same

○ length)
□ weight) where different

Prey diameter (cm)

1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0

0   2
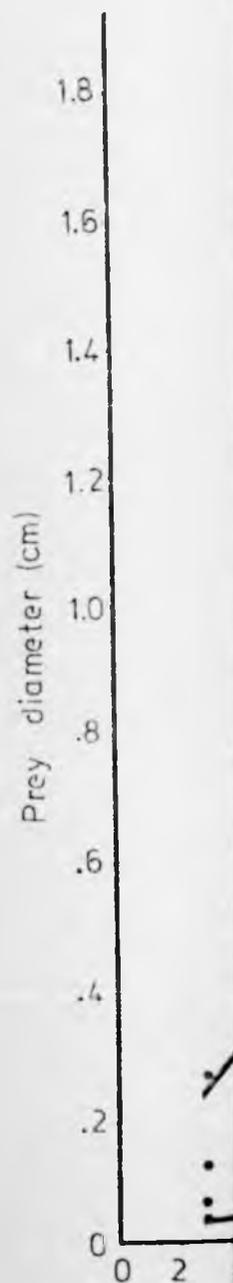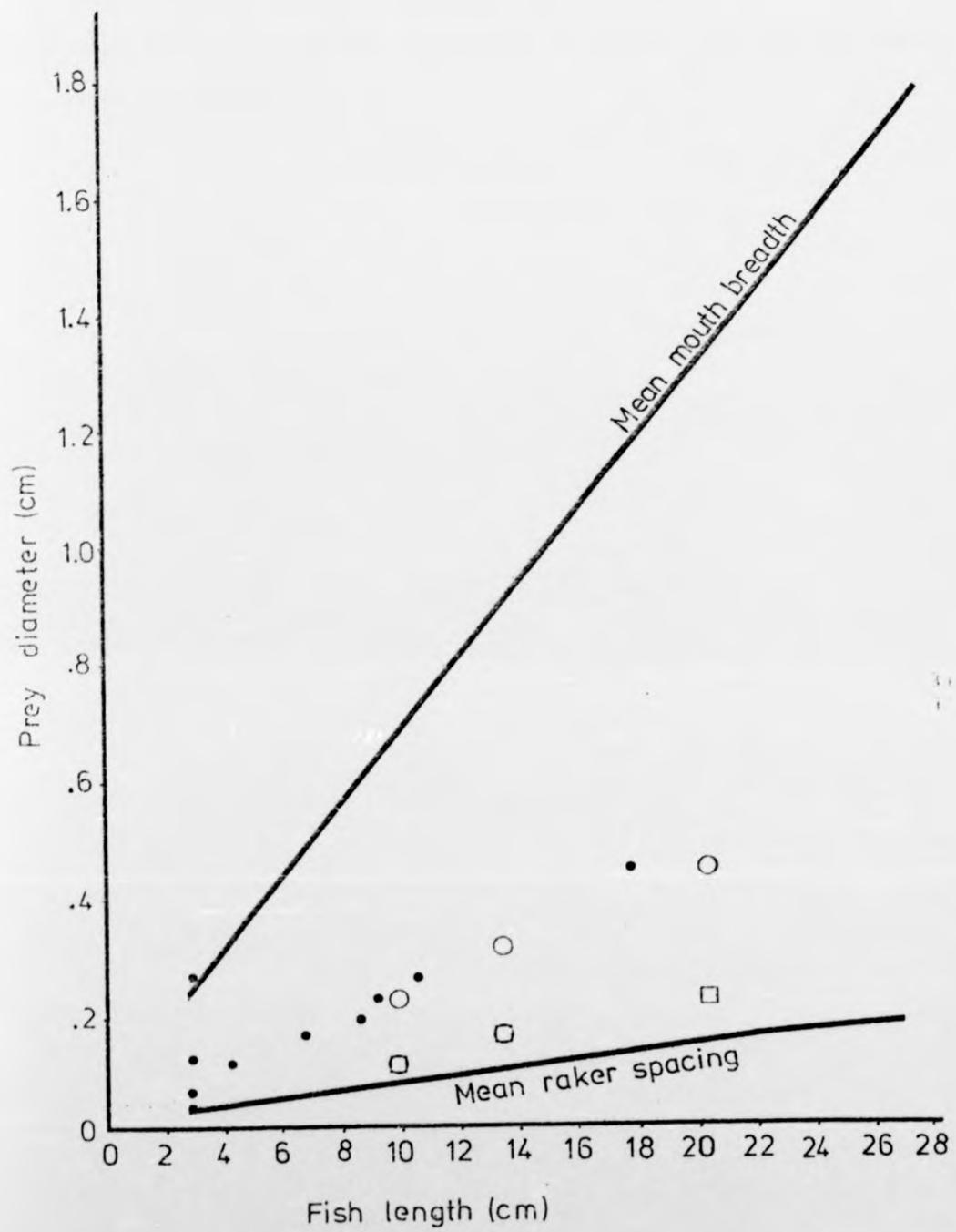
this would be of course, unnecessary, although field trials on the practicality of application of close feed particle size:fish size limits would be required.

APPENDIX

STOMACH CONTENTS

Since prey selectivity has characteristically been examined by comparison of the distribution frequency of prey in fish stomach contents with that in the environment it is relevant to examine this approach more closely. One study that provides sufficient information for re-analysis is that of Egglishaw (1967) on the food and growth of Atlantic salmon in the Shelligan burn. Since growth on particular prey sizes (and thus, by inference, selectivity) has already been shown to be seasonally variable, information from corresponding times of the year and fish of the same age must be examined. In June 0+ and 1+ salmon reached lengths of 3.5 and 7.0 cm respectively (Egglishaw, Fig. 1) fed selectively on the available prey (though not necessarily on the basis of body size). A wide range of prey genera were subsequently found in stomach samples (Table 8). Since most natural prey are elongate a consideration of prey length only (Egglishaw Table 9) may be misleading. It is unlikely that the major axis of a prey animal would govern its accessibility as salmon can be observed to ingest prey end-on in which orientation the greater of the minor axes would be the limiting dimension. In addition many prey organisms (e.g. Trichoptera, some Ephemeroptera, most Plecoptera) posses substantial appendages, in particular legs, that serve not only to increase their total visual size but also, due to limited movement of the proximal segments of each limb, their physical breadth.

Preserved examples of a wide range of prey organisms were measured and the ratios:

I) total body length (excluding appendages): total body breadth (excluding all appendages), and

II) total body length (excluding appendages): total breadth including limbs to the distal end of the femur where these were judged to consititute an impediment to ingestion were calculated (Table 1). The distribution frequency of prey by genus in the stomach contents of 0+ and 1+ salmon in June (Egglishaw, Table 8) was used to calculate weighted means of

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Table 1. Length: breadth conversion ratios.

Prey		Length:Breadth ratio	
		1 (excluding appendages)	11 (including limbs*)
		1:X	1:X
Plecoptera		0.25	0.4
Leuctra		0.2	0.4
Amphinemura		0.25	0.4
Isoperla		0.3	0.4
Ephemeroptera		0.4	0.6
Baëtis		0.3	0.5
Trichoptera		0.35	0.45
Hydroptila		0.4	0.4
Chironomidae,	larvae	0.15	0.15
	pupae	0.5	0.5
Coleoptera		0.5	0.6
Oreodytes		0.66	0.66

Notes: * see text
Plecoptera and Ephemeroptera - nymphs
Trichoptera - larvae
Coleoptera - adults

Weighted means:

0+ salmon	0.47	0.57
1+ salmon	0.37	0.51

the ratios I and II separately for 0+ and 1+ salmon. Thus the
distribution frequencies by breadth were calculated from the length
distributions from Table 9, and prey breadth:fish length ratios (analagous
to the P.F.R.) calculated. Figs. 1 and 2 (bottom) show calculated P.F.R.s
for:

    a)   prey length

    b)   prey (body) breadth (I)

    c)   prey (body + limbs) breadth (II)

and their distribution in stomach samples.

Since stomach content composition reflects some form of selection
the hypothesis can be put forward that it may be prey size-based and that
the greater minor axis (i.e. maximum breadth, II, where length is measured
along the major axis) determines selection. Comparison between the
selectivity behaviour (from Chapters 2 and 3) and stomach content size
distribution in terms of maximum breadth (II) of 1+ salmon in June (Fig.1)
shows:

    i) close correspondence between peaks

    ii) reduction in frequency of occurrence in stomachs corresponding
to (a) striking distance reduction (negative selectivity, p.132) with
decrease in prey size, and (b) decrease in the proportion of available
prey accepted with prey size increase above peak occurrence.
In addition the maximum breadth distribution frequency reaches zero
precisely at the P.F.R. corresponding to mean mouth breadth.

Since growth on particular prey sizes directly reflects prey
selection behaviour (p. 132) and is an index of prey suitability it can be
directly compared to the selection patterns implied by the stomach contents
size distribution (Fig. 1). The correspondence between peak prey occurrence
(maximum prey breadth) and peak growth rate is remarkable. In the absence
of behavioural data specific to 0+ fish, Fig. 2 compares growth response
(from Chapter 4) to prey size distribution. A similar correspondence
between the prey breadth distribution frequency and maximum growth response

FIG 1. Top - Striking distance, selection and
growth (8.6 cm, 1 + salmon, June).

    W% - percent change in weight

Bottom - Frequency of occurrence of
prey size classes in stomach
contents. (7.0 cm, 1 + salmon,
June)

From Egglishaw 1967, see text.

    - - -   by length
    ——   by breadth excluding all appendages
    ━━   by breadth including appendages

P.F.R. - Prey dimension: fish length ratio

—○— Striking distance
      (cm)

40

30

ΔW%   20

10

0

-10

-20

50

Relative   40

Frequency   30

20

10

0
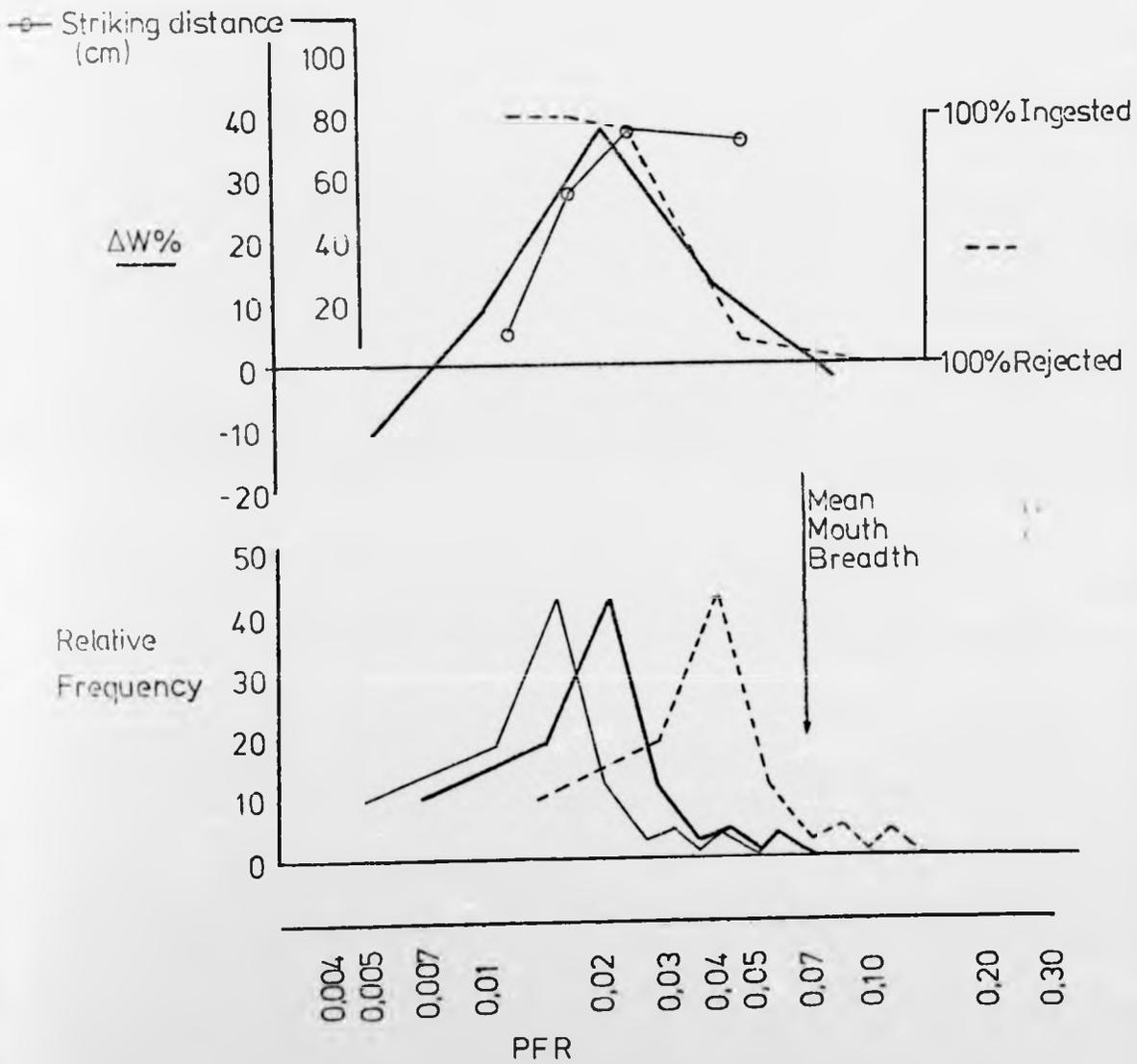
FIG 2. Top - Growth response (4.2 cm
          0 + salmon, July).

        W% - percent change in weight.

        Bottom - Frequency of occurence of
                 prey size classes in stomach
                 contents. (3.5 cm, 0 + salmon,
                 June).

        See Fig 1 for legend and source.

90

80

70

60

50

ΔW% 40

30

20

10

0

50

Relative 40

Frequency 30

20

10

0

ΔW%

Relative 40
Frequency 30

Mean
Mouth
Breadth

0.004
0.005
0.007
0.01
0.02
0.03
0.04
0.05
0.07
0.10
0.20
0.30

PFR
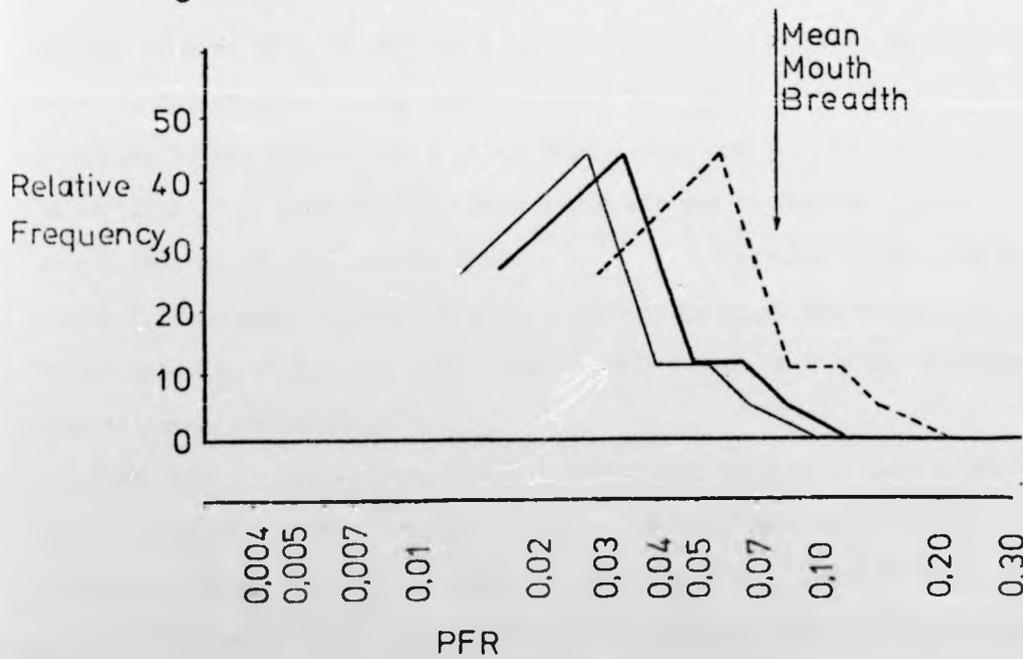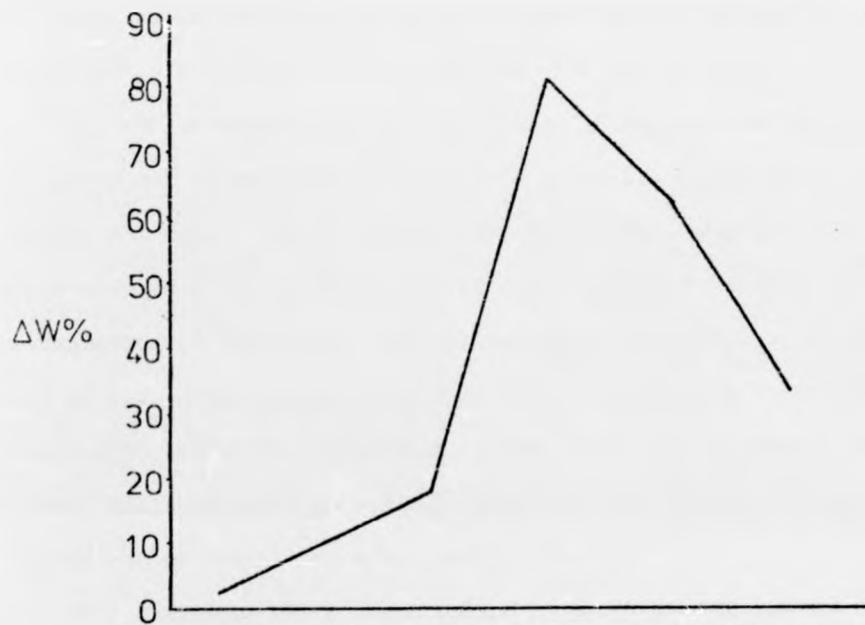
is shown, the good growth shown on larger prey sizes than optimum being reflected in the composition of stomach contents. Similarly the proposed ability of fish of this size-class to ingest prey larger than mouth breadth by means of jaw distention and continued manipulation (Chapter 4) is reflected in the presence of prey larger than mouth breadth, although a sharp tail-off in frequency occurs with this size of prey.

It can be argued that representation of stomach content composition by number cannot be directly related to potential growth rate. This is clearly not true if it is assumed that fish select prey in proportion to their requirements, in which case as a high growth rate requires maximisation of consumption efficiency selection would favour near-optimal prey sizes. However since prey body weight increases more or less exponentially with length the proportion of each size-class by weight in the stomach contents would potentially give a clearer picture of prey size related energy contribution to growth. However:

1) Residence times of different types of prey in the gut vary greatly (Thorpe 1977, 1) and there is evidence that this is in part size-related, larger natural prey (whose composition changes with size) remaining in the stomach for a longer period than smaller prey (Elliott 1972). In addition it is possible that larger prey may not be digested to the same extent as similar smaller prey. Therefore larger prey are likely to be overrepresented in stomach content analyses and their contribution in weight and energy terms over a period of time may be lower than indicated empirically.

2) The per capita occurrence of larger size classes of prey is in fact very small. Since the number of prey items per fish had a median value of 4 (range 0-14) in 1+ salmon in June (Egglishaw, Table 4) it is possible to predict the occurrence of different size classes in fish stomachs. Thus one prey in the 0.5 cm length class (maximum breadth P.F.R. 0.037) would occur once in 8.3 fish, and in the 0.7 cm class (0.051) only once in 25 fish. In comparison 1.7 prey in the 0.3 cm length class (0.022 P.F.R.,

ie peak) would be expected in each fish (1 in 0.6). Therefore large
organisms represent only a very occasional ingestion in comparison to
smaller items, and at any one sampling occur in a very small proportion
of fish stomachs. This view is supported by the great variation in
stomach content weight, both within one sample and between sampling
periods (Table 4, eg 21.3 fold, O+ fish in June; 14.4 fold in August),
since the occasional inclusion of a large prey item would account for
this level of variation between stomachs.

Therefore, in summary, larger prey sizes are not only likely to be
overrepresented but bulked distribution frequency results overemphasise
their importance to individual fish. It is therefore clearly impractical
at this stage to speculate on the relationship between individual prey
weight and its contribution to growth. The relationship between prey
composition, thus possible selection, and behavioural selectivity afford
the best approach to separating morphometric selection from specific
preferences when dealing with stomach contents.

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